

**Revision of the genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae), with descriptions and comments on other species described in *Leonnates***

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**Abstract.**—The genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae) is characterized by the presence of both papillae and paragnaths on the pharynx, and either only spinigers or spinigers and falcigers on the notopodia. Although the identity of several *Leonnates* species is in doubt, no systematic revision of the genus has been undertaken. In this study, we examine the validity of the following species that have been described as *Leonnates* or are related to *Leonnates*: *L. indicus* Kinberg, 1866, *L. virgatus* Grube, 1873, *L. pusillus* Langerhans, 1880, *L. jousseaumei* Gravier, 1899, *Australonereis ehlersi* (Augener, 1913), *L. niestraszi* Horst, 1924, *L. decipiens* Fauvel, 1929, *L. insolitus* Gravier & Dantan, 1934, *L. simplex* Monro, 1939, *L. persicus* Wesenberg-Lund, 1949, *Paraleonnates uschakovi* Chlebovitsch & Wu, 1962, *L. decipiens* var. *manilensis* Pillai, 1965, *L. stephensoni* Rullier, 1965, *Websterinereis glauca* Pettibone, 1971, *L. nipponicus* Imajima, 1972, *L. crinitus* Hutchings & Reid, 1991, and *L. bolus* Hutchings & Reid, 1991. Our examination of available type specimens and additional material shows that *L. virgatus* and *L. jousseaumei* are conspecific with *L. indicus*; *L. decipiens* var. *manilensis* is conspecific with *L. decipiens*; *Leonnates bolus* belongs to *Paraleonnates*; *Leonnates niestraszi*, and *L. insolitus*, described from heteronereidid specimens, can not be fully characterized. *Leonnates nipponicus* was not available for examination; its original description indicates a distinct difference from *L. indicus*. Characters of *A. ehlersi*, originally described in the subgenus *Leonnates* in *Nereis*, are discussed. *Leonnates pusillus* is indeterminable to genus. Some specimens originally identified as *L. jousseaumei* are heteronereidids of *Perinereis*. Descriptions of *Leonnates* and related species and a key to atokous *Leonnates* species are provided.

In the original description of the genus (Kinberg 1866), the following characters were used to define *Leonnates*: pharyngeal areas I and V smooth; pharyngeal areas II, III, IV with paragnaths; pharyngeal areas VI, VII–VIII with papillae; anterior and posterior parapodia similar; dorsal and ventral rami separate; with compound spinigers and falcigers; and dorsal cirri not foliaceous.

To date, fourteen species and one variety have been described in the genus, all from

tropical or subtropical coastal areas. There are a number of problems with the described species. The type species, *L. indicus*, was described only briefly and has been considered dubious or unrecognizable by some workers (e.g., Horst 1924, Monro 1939). A number of synonymies between the described species have been suggested, although without convincing evidence [e.g., between *L. indicus* and *L. jousseaumei* by Monro (1931) and between *L. jousseaumei* and *L. virgatus* by Hartman (1959)]. Two

of the species, *L. niestraszi* and *L. insolitus*, were described only from heteronereidid specimens, which have significantly modified parapodia and setae. Three other described species, *L. pusillus*, *Nereis* (*Leonnates*) *ehlersi*, and *L. bolus*, do not belong to the genus at all.

Some original characters defining the genus are also in doubt. The pharynx of *Leonnates* together with *Paraleonnates* Chlebovitsch & Wu, 1962 is characterized by the presence of soft papillae on the oral ring and paragnaths on the maxillary ring. However, papillae were described on area IV of the maxillary ring in *L. virgatus* Grube, 1873 and *L. nipponicus* Imajima, 1972, and Monro (1931) and Hutchings & Reid (1991) noted partially hardened paragnaths on area IV of *L. jousseaumei* Gravier, 1899. Furthermore, the setae in the described species of *Leonnates* are predominantly homogomph spinigers and falcigers, which have been described with a variety of terms (Monro 1939, Wesenberg-Lund 1949, Pillai 1965, Rullier 1965, Hutchings & Reid 1991). Some of these terms refer to the same type of seta [e.g., the falcigers of *L. persicus* were said to be heterogomph and fairly heterogomph by Wesenberg-Lund (1949) and slightly heterogomph by Rullier (1965)].

The aim of this study is to address these problems, to redescribe valid species, whenever possible, on the basis of type and non-type material and to redefine the genus *Leonnates*.

#### Materials and Methods

Line drawings were made with the aid of a camera lucida attached to a stereomicroscope or a video camera attached to a compound microscope. Parapodia used for scanning electron microscopy (SEM) were transferred sequentially from 70% ethanol to de-ionized water, frozen in liquid nitrogen, freeze-dried with a Virtis 12SL drying unit, gold-coated with a Denton Vacuum

Desk II sputter coater, and observed using a JOEL 6300 SEM.

The names of the following institutions are abbreviated in the text: Australian Museum, Sydney (AM); The Hong Kong University of Science and Technology (HKUST); Institute of Oceanology, Chinese Academy of Science, Qingdao (IOCAS); Museum of Natural History, Wroclaw University (MNHUW); Muséum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); National University of Singapore (NUS); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); The Natural History Museum, London (BMNH); Natural History Museum, Vienna (NHMV); Northern Territory Museum of Arts and Sciences, Darwin, Australia (NTM); Queensland Museum, Brisbane, Australia (QM); Swedish Museum of Natural History, Stockholm (SMNH); Western Australian Museum, Perth (WAM); Zoological Museum, University of Copenhagen (ZMUC); Zoological Institute and Zoological Museum, University of Hamburg (ZIM); Zoological Museum Amsterdam, University of Amsterdam (ZMA).

#### Systematics

##### *Leonnates* Kinberg, 1866

*Leonnates* Kinberg, 1866:168; Imajima 1972:41; Fauchald 1977:89; Wu et al. 1981:65; Hutchings & Reid 1991:48.

Type species: *Leonnates indicus* Kinberg, 1866 (by monotypy).

*Diagnosis*.—Eversible pharynx with pair of jaws, soft papillae and occasionally paragnaths on oral ring, paragnaths and occasionally soft papillae on maxillary ring. Prostomium with pair of antennae, pair of biarticulate palps and 2 pairs of eyes. Peristomium with 4 pairs of tentacular cirri. Parapodia biramous, except first 2 pairs. Notopodia with dorsal notopodial ligule, infra-acicular ligule, and often supra-acicular ligule. Neuropodia with presetal acicular

lobe or ligule, postsetal lobe or ligule, and ventral ligule. Notosetae homogomph spinigers and occasionally homogomph falcigers. Neurosetae homogomph or heterogomph spinigers and homogomph or heterogomph falcigers. By SEM, ends of the setal shaft with a large solitary tooth and a circular fringe of smaller teeth.

The currently accepted generic definition of *Leonnates* (e.g., Fauchald 1977) includes the following: pharynx with papillae on the oral ring and paragnaths on the maxillary ring; four pairs of tentacular cirri; biramous parapodia; notosetae homogomph spinigers; neurosetae heterogomph falcigers. Most *Leonnates* species share these features. However, this definition has not taken into account the variation of some of the characters. The papillae on area IV of the maxillary ring of *L. indicus* can be sclerotized to different extents. Paragnaths are present on area VI of the oral ring of *L. simplex*. In addition to spinigers, falcigers are also present on the posterior notopodia of *L. indicus*. Although the neuropodial falcigers of *L. decipiens*, *L. simplex*, and *L. crinitus* are heterogomph, in other species they are homogomph. Some parapodial characters shared by all *Leonnates* species are not included in the generic definition. The neuropodial acicular lobe of *Leonnates* consists of a rounded presetal lobe or a conical presetal ligule and a postsetal ligule or postsetal lobe. The generic diagnosis was, therefore, emended to accommodate these features. This change, however, does not affect its relationship with other nereidid genera.

*Leonnates indicus* Kinberg, 1866  
Figs. 1–3; Table 1

*Leonnates indicus* Kinberg, 1866: 168.

*Leonnates virgatus* Grube, 1873: 68.

*Nereis (Leonnates) virgata* Grube, 1878: 63–64, pl. 4, fig. 7.

*Leonnates Jousseaumi* Gravier, 1899: 234–237.

*Leonnates Jousseaumei* Gravier 1901: 160–

164, pl. 11, figs. 34–37; text-figs. 162–165.

*Leonnates jousseaumei*. Fauvel 1919: 400; Horst 1924: 150; Fauvel 1930: 19, fig. 5A–E; Monro 1931: 43–44, fig. 4A; Fauvel 1932: 85; Monro 1939: 403; Fauvel 1953: 169–170, fig. 86D–F; Day 1967: 330–331; Wu et al. 1981: 67–68, fig. 38; Hutchings & Reid 1991: 52–53.

*Material examined.*—*Leonnates indicus*: holotype from Knoll, Singapore (SMNH 535); *L. virgatus*: the Philippines, coll. Semper (1 holotype or syntype); *L. jousseaumei*: Obock, Red Sea, 1895, coll. Jousseaume (14 syntypes) (MNHN A78); Suez Gulf and Canal, 1928 & 1933, coll. Fauvel (7 specimens) (MNHN A304); Strait of Makassar, St. 14, 25–34 m, 16 Dec 1908, coll. van Kampen (1 specimen) (ZMA V. Pol. 535); Siboga Expedition St. 164, East of Misool (1°42'30"S, 130°47'30"E) (2 specimens); St. 213, Saleyer anchorage and surroundings, reef (1 specimen); St. 273, Anchorage off Pulu Jedan, east coast of Aru Islands, 13 m (1 specimen); St. 315, Anchorage East of Sailus Besar, Paternoster Islands (1 specimen) (above 5 specimens in ZMA V. Pol. 536); Fenelon Island (14°02'S, 125°43'E), 6 m, 8 Feb 1988, coll. Hutchings (1 specimen) (AM W202841); Princess Charlotte Bay, Queensland (14°07'S, 143°09'E), 12–15 m, Prawn Trawl, 23 Feb 1979 (1 specimen) (AM W202842); Xincun, Hainan Province, China, 1–3 m, coral, 26 Mar 1992, coll. Sun (4 specimens) (HKUST W0002–W0005).

*Redescription based on the holotype of Leonnates indicus.*—Holotype consisting of 4 fragments, likely from single specimen forming complete worm. Left parapodium of setiger 7 dissected by previous researcher and kept separately. From anterior end, fragment containing 7, 20, 20, and 11 setigers, respectively, for 58 setigers.

Animal colour cream, with darker cream parapodial glands at base of notopodial ligule. Prostomium pentagonal, frontal part including antennae missing (Fig. 1A). Two



pairs of eyes, black with distinct lenses arranged trapezoidally, anterior pair slightly larger. Palps thick, cylindrical, each with small palpostyle. Peristomium tentacular cirri slender, longest reaching setiger 7 (one cirrus on each side missing).

Pharynx everted. Jaws brownish, smooth. Maxillary ring with paragnaths and soft papillae arranged as follows: area I = 0; II = sharp paragnaths, 6 left, 5 right, each in small cluster; III = 3 small soft papillae in transverse row; IV = paragnaths, tips worn off, 6 left, 7 right, each in small cluster. Oral ring with only soft papillae, larger than those on area III: area V = 0; VI = 8 left, 9 right, conical, each in small cluster; VII–VIII = 74, conical, irregularly arranged in 3–4 rows (Fig. 1B).

Parapodia of first 2 setigers uniramous, without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 1C). Dorsal notopodial ligule conical, swollen at base, slightly shorter than dorsal cirrus. Neuropodial presetal acicular ligule conical, smaller than neuropodial postsetal ligule. Ventral neuropodial ligule conical, swollen at base. Dorsal cirrus slender, extending beyond dorsal notopodial ligule; ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Figs. 1D, 2A–C). Dorsal notopodial ligule conical, swollen at base, with yellowish glandular region. Notopodial supra-acicular ligule gradually reduced along body (Fig. 2A, B), disappearing by setiger 51 (Fig. 2C). Notopodial infra-acicular ligule becoming slightly smaller along body, but distinct on posterior segments. Dorsal cirrus slender, extending beyond dorsal notopodial ligule. Neuropodial presetal acicular ligule projecting ventrolaterally, shorter than neuropodial postsetal lig-

ule (Figs. 1D, 2A, B). Ventral neuropodial ligule smaller than but approximately as long as neuropodial presetal acicular ligule. Ventral cirrus subulate, about as thick but much shorter than dorsal cirrus.

Two anal cirri present, extending for length equivalent to 6 posterior setigers.

Notopodia with homogomph spinigers and homogomph falcigers. Spinigers with slender blade (50–150  $\mu\text{m}$  long) fringed on cutting edge; larger tooth at end of shaft, facing cutting edge of blade, approximately as long as circular fringe of smaller teeth (Fig. 3A), present throughout body. Falcigers about 25  $\mu\text{m}$  long, with coarsely serrated, convex blade ending with pointed tip; tooth at end of shaft facing cutting edge of blade, approximately as long as circular fringe of slender teeth. Six falcigers observed on posterior notopodia (one on each parapodium: left setigers 51, 52, 53, 56, and right setigers 52, 53). Neuropodia with similar spinigers and falcigers. Spinigers present from setiger 3. Falcigers (Fig. 3B) present throughout body, numbering 2–20 per neuropodium.

Female, parapodia with numerous oocytes, 100–105  $\mu\text{m}$  diameter. Parapodia and setae sexually unmodified.

*Remarks.*—The holotype of *L. indicus* is in poor condition. The frontal part of the prostomium has been damaged and the antennae are now missing. Most coelomic fluid is lost. Some setal blades are missing, which makes it difficult to determine the setiger where notopodial falcigers are first present. However, the remaining 6 falcigers observed on the notopodia of setigers 52–56 suggest that their occurrence starts in the posterior segments. Left parapodium 7 was used for SEM (Fig. 3A, B) after use for a line drawing (Fig. 1D).

The holotype or syntype of *L. virgatus*, originally dried, was rehydrated in 75% ethanol. It consists of an anterior fragment of 20 setigers and a middle fragment of 30 setigers. Animal colour is greyish with darker pigmentation on the palps, prostomium, bases of parapodia, and dorsum (Fig. 2D).



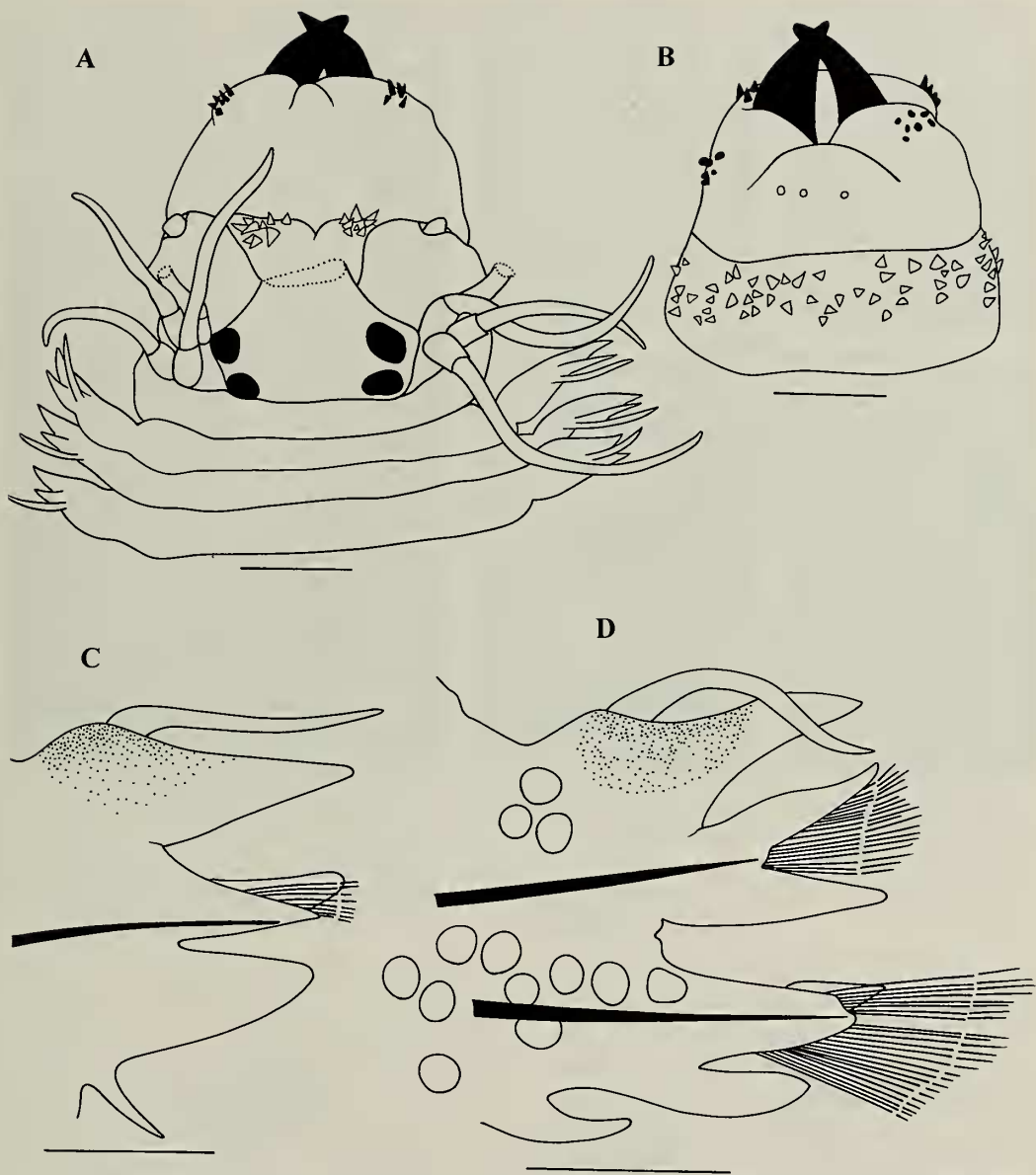


Fig. 1. *Leonnates indicus* (Holotype SMNH 535). A. Dorsal view of anterior region. B. Ventral view of pharynx. C. Anterior view of parapodium 2. D. Anterior view of parapodium 7. (Scale: A, B, D = 0.5 mm; C = 0.25 mm).

The prostomium is pentagonal with a pair of antennae and 2 pairs of uncoloured eyes. Jaws are brownish and smooth. The maxillary ring of the everted pharynx has chitinized paragnaths and soft papillae as follows: area I = 0; II = paragnaths, 5 on left, 6 on right, each in a small cluster; III = 4

small soft papillae, in a transverse row; IV = paragnaths, 7 on left, 5 on right, each in a small cluster. The oral ring has only soft papillae, larger than those on area III as follows: V = 0; VI = 5 on each side, conical, each in a cluster; VII–VIII = 27, conical, irregularly arranged in 2 rows (Fig. 2D, E).

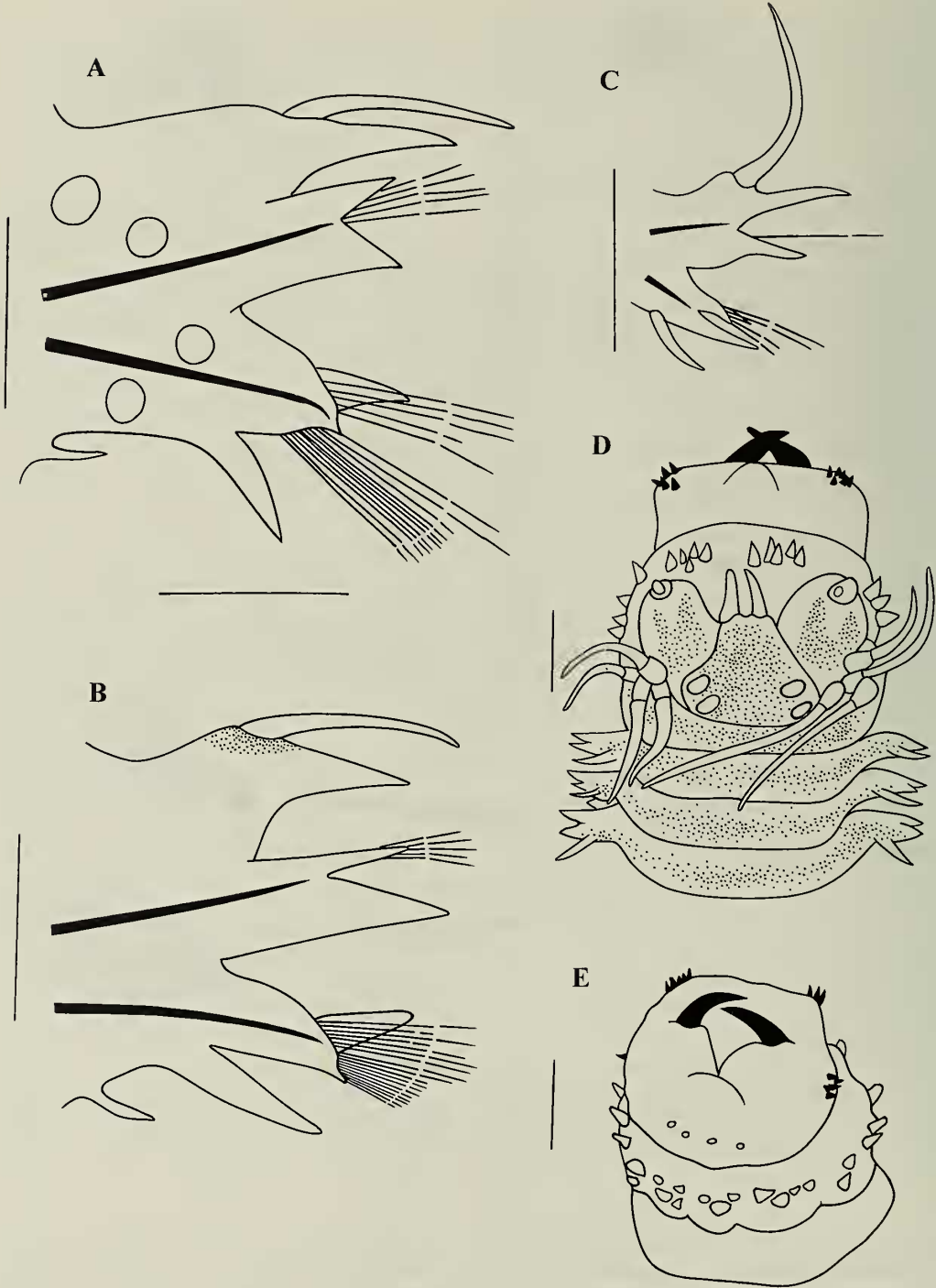


Fig. 2. *Leonnates indicus* (A–C: Holotype SMNH 535; D–E: MNHWU 322). A. Anterior view of parapodium 20. B. Anterior view of parapodium 47. C. Anterior view of parapodium 53. D. Dorsal view of anterior region. E. Anterior view of pharynx. (Scale: A–E = 0.5 mm).

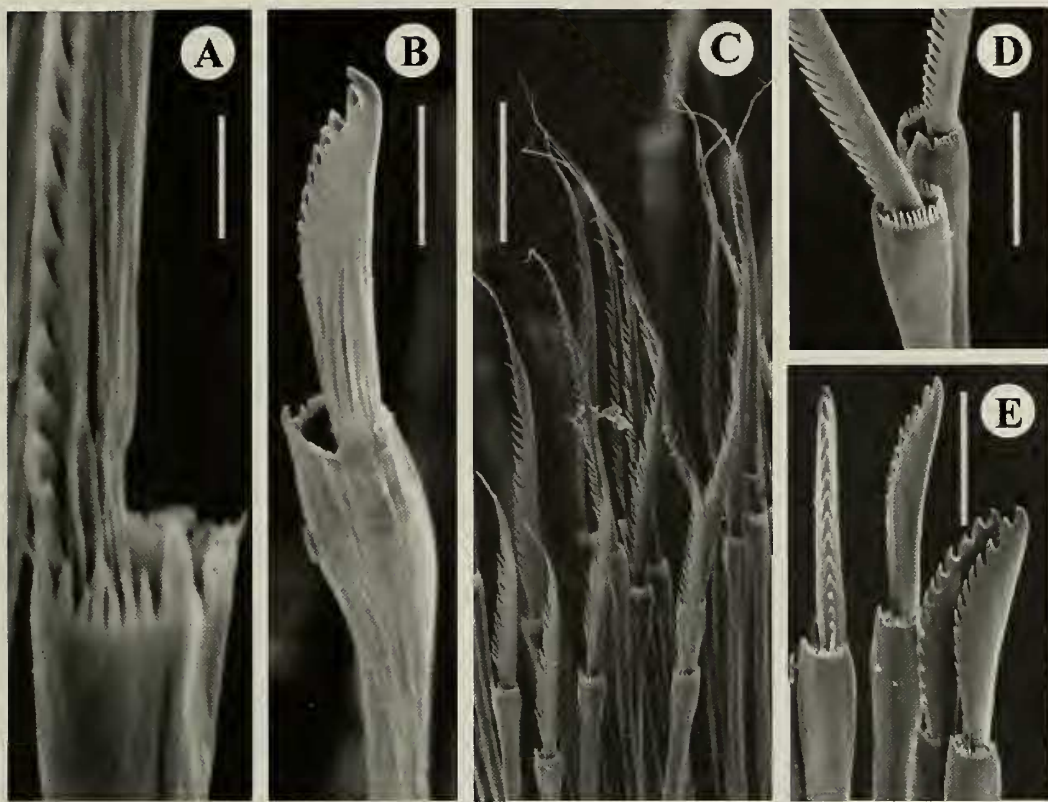


Fig. 3. *Leonnates indicus* (A–B: Holotype SMNH 535; C–E: HKUST W0005). A. Notopodial spiniger from parapodium 7. B. Neuropodial falciger from parapodium 7. C. Notopodial spinigers from parapodium 31, showing blades different in length. D. Enlarged ends of shaft of another two notopodial spinigers from parapodium 31. E. Neuropodial falcigers in different orientations from parapodium 31. (Scale: A = 3  $\mu\text{m}$ ; B = 10  $\mu\text{m}$ ; C = 30  $\mu\text{m}$ ; D = 10  $\mu\text{m}$ ; E = 30  $\mu\text{m}$ ).

The pharyngeal armature of the type of *L. virgatus* is very similar to that of the holotype of *L. indicus*, except the latter has more papillae on areas VII–VIII. The shapes of the parapodia of *L. indicus* and *L. virgatus* are also similar, except, in the latter, the notopodial supra-acicular lobe is absent from the middle region (setiger 20) while in the former it is absent from the posterior region (setiger 51) (Table 1). This difference could be an artifact of the long dehydration of *L. virgatus*, since the notopodial supra-acicular lobe is small in the middle and posterior regions and the rehydration may not have made this once-existing structure visible. There is also some mucus-like material covering part of the notopodia, making observation difficult.

The blades of most setae are broken off. Setae with intact blades that remain are of the same types as those found in the holotype of *L. indicus*. Notopodia have homogomph spinigers throughout and 1 homogomph falciger was observed on right setiger 50. Neuropodia have homogomph spinigers from setiger 3 and homogomph falcigers throughout.

Grube (1873) described *L. virgatus*, based on apparent differences from the brief and somewhat inaccurate description of *L. indicus*; his specimen had no incision on the frontal margin of the prostomium, dorsal cirri were longer than dorsal notopodial ligules, and the peristomium was longer than the next three segments. Our observation confirms that the type specimen



Table 1.—Diagnostic characteristics of *Leonnates indicus*. Numbers following original catalogue numbers are added to distinguish the specimens in the same lot. Numbers of processes on the left side and right side of areas II, IV and VI are separated by a slash. Maxillary ring: P = papillae; S = sclerotised papillae; PS = partially sclerotised papillae; N/A = damaged, indeterminate; other numbers represent paragnaths. NSL (notopodial supra-acicular ligule): N/A = posterior region missing or modified, not available for examination.

Specimen cat. no.	Sex	Size (mm)	Maxillary ring				Oral ring papillae			Absence of NSL from setiger	No. of setigers	Notopodial falcet(s) present on setiger(s)
			I	II	III		IV	V	VI	VII–VIII		
SMNH 535	F	3.3 × 24	0	6/5	3P		6/8	0	8/9	74, 3–4 rows	51	58
ZMA 535	F	6.5 × 54	0	6/5	7S		6/8	0	9/10	112, 4–5 rows	73	81
MNHN A78.1	F	6.0 × 55	0	4/4	8P		3/3	0	12/11	75, 3–4 rows	76	79
MNHN A78.2	N/A	5.3 × 43	0	6/4	6P		10/11	0	5/7	111, 4–5 rows	56	62
MNHN A78.3	N/A	4.3 × 36	0	9/8	7P		14/9	0	7/11	46, 3 rows	57	65
MNHN A78.4	N/A	4.2 × 31	0	7/5	6PS		7/11	0	6/8	62, 3 rows	71	76
MNHN A403.1	N/A	2.3 × 12	0	4/5	3P		4/4	0	4/4	23, 2 rows	16	56
MNHN A403.2	N/A	4.5 × 28	0	3/5	3P		7/7	0	12/15	81, 3–4 rows	57	65
MNHN A403.3	N/A	5.5 × 62	0	8/8	5P		8/9	0	11/9	85, 3–4 rows	79	84
Siboga 164.1	N/A	4 × 6	0	7/8	6P		14/8	0	11/8	48, 3 rows	N/A	16*
Siboga 164.2	N/A	3.2 × 9	0	7/5	4P		7/8	0	5/5	33, 2 rows	N/A	23*
Siboga 273	N/A	3.7 × 29	0	5/5	5P		6/8	0	8/6	59, 3 rows	56	69
AM W202841.1	F	2.5 × 19	0	5/6	N/A		5/6	0	6/5	22, 2 rows	48	53*
AM W202841.2	N/A	2 × 15	0	6/5	3P		7/7	0	6/6	15, 2 rows	14	61
AM W202842	N/A	7 × 48	0	14/10	8PS, 2 rows		16/18	0	15/18	91, 4–5 rows	N/A	43*
MNHWU 322	N/A	2.3 × 15	0	5/6	4P		7/5	0	5/5	27, 2 rows	20	51*
HKUST W0002	N/A	4.2 × 43	0	5/7	6P		10/11	0	13/11	83, 3 rows	78	83
HKUST W0003	F	4 × 32	0	6/6	4S		5/7	0	12/9	62, 3 rows	66	72
HKUST W0004	N/A	3.8 × 27	0	18/17	8PS, 2 rows		19/20	0	15/12	84, 4 rows	58	66
HKUST W0005	N/A	4 × 28	0	9/9	6PS		11/12	0	14/12	57, 3–4 rows	62	66

\* incomplete.

of *L. virgatus* has no incision on the frontal margin of the prostomium, which on the holotype of *L. indicus* is missing. However, in none of the other material of *L. indicus* examined is the frontal margin of the prostomium incised. Moreover, in all material examined, the dorsal cirri are longer than the dorsal notopodial ligules. The peristomium is longer than the next three segments on the type of *L. virgatus* only on the ventral side where the lengths of the peristomium and setigers 1 to 3 are 0.40, 0.16, 0.16, and 0.20 mm, respectively; on the dorsal side, however, these segments are of similar lengths, measuring 0.24, 0.24, 0.28, and 0.28 mm, respectively. On the holotype of *L. indicus*, and on all other non-type *L. jousseaumei* material examined, the peristomium and the first 3 setigers are also of similar length on dorsal side, while the peristomium is much longer on ventral side.

The original descriptions of *L. jousseaumei* (Gravier 1899, 1901) were quite detailed, but Gravier did not state on what basis he separated *L. jousseaumei* from *L. indicus* and *L. virgatus*. The pharyngeal armature of *L. jousseaumei* resembles that of the holotype of *L. indicus*, except the former has 3–8 paragnaths, rather than 3 papillae, on area III (Fig. 1B, Table 1). Different extent of scleritization of papillae on pharyngeal area III of *L. jousseaumei* have been reported and discussed (Fauvel 1919, Hutchings & Reid 1991), and our observation reveals that this phenomenon is common among specimens collected from the same populations (Table 1). The extent to which the papillae on area III are sclerotized does not seem to be associated with the size of the specimen because the papillae of the specimens from the same locality (Xincun, Hainan Province), which are of similar size, vary from soft to completely sclerotized (Table 1). The occurrence of paragnaths on area III (Gravier 1899), therefore, does not sufficiently separate *L. jousseaumei* from *L. indicus* or *L. virgatus*.

Gravier (1899) divided the setae of *L. jousseaumei* into three types: slightly het-

erogomph spinigers with a long and slender cutting edge; almost homogomph falcigers with a distinctively serrated convex cutting edge; and homogomph falcigers with straight thin blade. Later authors (Fauvel 1953, Hutchings & Reid 1991) only recognized two types of setae: homogomph spinigers and homogomph falcigers. As the orientation of a seta affects whether the end of the shaft looks symmetrical or slightly asymmetrical to the long axis of the shaft, the 'slightly heterogomph' and 'almost homogomph' setae (Gravier 1899) are both likely to be homogomph setae (cf., Fig. 3C, showing, at lower left corner, some falcigers with a large tooth slightly longer than the surrounding fringes at the end of the shaft; Fig. 3D, showing another two spinigers that looked perfectly homogomph at higher magnification). Similarly, the orientation of a seta also affects whether its blade looks thin or wide (Fig. 3E). The second and third types of setae of Gravier (1899) are thus considered as likely to be identical.

Gravier (1899) reported the occurrence of falcigers both notopodially and neuropodially on setiger 25, without noting the distribution of falcigers along the body. Monro (1931), Fauvel (1953), and Hutchings & Reid (1991) indicated that falcigers are present on all neuropodia as well as on posterior notopodia. Among the material examined, the most anterior notopodium containing a falciger is setiger 25. Notopodial falcigers were observed only on a few posterior setigers, probably because only a few such setae on each posterior notopodium and they are often broken or with their blades missing.

Siboga Stations 213 and 315 (see Horst 1924) each contains a heteronereidid male specimen with an inverted pharynx. They were assigned to *L. jousseaumei* by Horst (1924) and were subsequently cited by Imajima (1972). The two specimens are quite similar. The pharynx of the specimen from St. 315 has been dissected and is now missing. The specimen from St. 213 has 172 setigers that are divided into two regions:

the anterior 21 setigers and the remaining 151 setigers. The anterior region is not modified, except on the first 7 setigers the bases of the dorsal cirri are swollen. The parapodia of the posterior region are highly modified, having thin accessory flaps in both notopodia and neuropodia and a crenulated lower edge on the dorsal cirrus. The pygidium has a rosette of papillae and two anal cirri. A dissection of this specimen reveals paragnaths, but no papillae, on the pharynx. Therefore, it is not *Leonnates*. The paragnaths are arranged as follows: area I = 1, conical; II = 8, conical, in a cluster; III = 31, conical, in 3 rows; IV = 23–26, conical, in a crescent; V = 1, conical; VI = 2, slightly curved long flat teeth; VII–VIII = 42, conical, in 2 rows. The pharyngeal armature, the parapodia and the setae in the anterior region suggest that this specimen belongs to *Perinereis*. It resembles *Perinereis singaporiensis* Grube, 1878 (sensu Horst 1924: 168–170, pl. 34, figs. 1–2), except that there is only one paragnath (instead of two) on area I, and there are no conical paragnaths between the two elongated teeth on area VI.

Our observation shows that the pharyngeal armature, prostomium, parapodia, and setae of *L. virgatus* and *L. jousseaumei* all resemble those of *L. indicus*; therefore, they are considered to be conspecific. The original description of *Leonnates indicus* (Kinberg, 1866: 168) is unclear, somewhat inaccurate, not accompanied by a figure, and based on one specimen. This has contributed to the erection of the synonyms *L. virgatus* and *L. jousseaumei* for the same species. Specimens of *L. indicus* vary greatly in size (2–7 mm wide by 15–54 mm long) (Table 1). The pharyngeal armature is consistent in having smooth areas I and V, but on other areas there is variation in number of papillae or paragnaths as follows: II = 4–18 paragnaths; III = 3–8 papillae or paragnaths; IV = 3–20 paragnaths; VI = 5–18 papillae; VII–VIII = 15–112 papillae. The number of papillae on area VII–VIII seems to be related to body size as larger speci-

mens usually have more papillae [ $Y = 17.4X - 9.22$ ,  $Y$  = number of papillae on areas VII–VIII,  $X$  = body width (mm),  $n = 20$ ,  $r = 0.837$ ]. Although the 5 females examined (Table 1) differ substantially in size, they all contain oocytes of approximately the same size (diameter 100–105  $\mu\text{m}$ ) and show no signs of heteronereidid modification.

*Habitat*.—Not mentioned in the original description of the holotype. Other specimens collected from depths of 25–24 m (Horst 1924), 60 m (Monro 1931), and 6–64 m (Hutchings & Reid 1991) were found among coral debris (Hutchings & Reid 1991), co-existing with *Ceratonereis erythraeensis* Fauvel, 1918, or among corals and sponges (Wu et al. 1981).

*Distribution*.—Australia; Indonesia; Singapore; Malaysia; the Philippines; Hainan; Macassar Strait; Bay of Bengal; Arabian Sea; Persian Gulf; Red Sea.

*Leonnates niestraszii* Horst, 1924

Figs. 4, 5

*Leonnates niestraszii* Horst, 1924: 150–151, figs. 4, 5.

*Material examined*.—Syntypes, Anchorage of North Ubian (6°7'30"N, 120°26'E), Siboga Expedition St. 99, surface, (2 complete specimens) (ZMA V. Pol. 537), (2 anterior fragments and 3 posterior fragments) (ZMA V. Pol. 538).

*Description*.—The two complete specimens in ZMA V. Pol. 537 measure 1.5 by 7.3 mm for 50 setigers and 2.4 by 9 mm for 55 setigers, respectively. The original description was based on the specimen with an everted pharynx in ZMA V. Pol. 537. Unless otherwise stated, our description is based on this specimen.

Body short with 2 distinctive regions: slightly modified anterior region consisting of 11 setigers and significantly modified posterior region.

Prostomium pentagonal (Fig. 4A), not cleft on frontal margin, with pair of short antennae and pair of biarticulate palps. Two



pairs of enlarged eyes arranged trapezoidally. Peristomium with dorsal tentacular cirri missing. Longest dorsal tentacular cirri reaching setiger 6 on the other specimen of the same lot.

Pharynx everted (Fig. 4A, B). Jaws brownish, with 6–7 denticles. Maxillary ring with paragnaths and papillae arranged as follows: area I = 0; II = paragnaths, 5 left, 3 right; III = 3 tiny papillae, in transverse row; IV = paragnaths, 4 left, 4 right. Oral ring with papillae arranged as follows: area V = 0; VI = 4 left, 6 right, each in 1 small cluster; VII–VIII = 12 in 2 irregular rows.

Parapodia of first 2 setigers uniramous, without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 4C). Dorsal notopodial ligule conical. Neuropodial presetal acicular ligule conical, smaller than postsetal ligule. Dorsal cirrus swollen at base, longer than parapodial ligules. Ventral neuropodial ligule longer than neuropodial presetal acicular ligule, shorter than dorsal notopodial ligule. Neuropodial cirrus slightly swollen at base, shorter than parapodial ligules.

Remaining parapodia of anterior region biramous, with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 4D). Dorsal notopodial ligule conical. Notopodial supra-acicular ligule extending about as far as dorsal notopodial ligule, infra-acicular ligule slightly smaller. Neuropodial presetal acicular ligule short, conical, slightly shorter than neuropodial postsetal ligule. Ventral neuropodial ligule conical, not extending as far as neuropodial ligules. Dorsal cirri of setigers 3–7 and ventral cirri of setigers 3–5 also swollen at bases.

From setiger 12, parapodia greatly modified with thin accessory flaps. Dorsal side at base of dorsal cirrus with broad flap, dorsal notopodial ligule expanded, notopodial

infra-acicular ligule expanded, neuropodial postsetal lobe broad and fan-shaped, ventral neuropodial ligule expanded, base of ventral cirrus with broad flaps on dorsal and ventral sides. Dorsal cirrus and ventral cirrus slender (Fig. 4E).

Pygidium surrounded by rosette of papillae; anal cirri missing.

Notopodia with two types of setae: homogomph spinigers on setigers 3–11 and paddle-shaped setae from setiger 12 on. Some spinigers (Fig. 5A, B) modified with short blade and slightly bent shaft tip; others similar to those of *L. indicus* in Fig. 3 (Fig. 5C, D). Paddle-shaped setae with minute serrations on one of two convex edges of blade; end of shaft not fringed with slender teeth (Fig. 5F). Neuropodia with 3 types of setae: homogomph spinigers, paddle-shaped setae, and homogomph falcigers. Spinigers and paddle-shaped setae similar to those in notopodia. Spinigers present in neuropodia 3–11. Falcigers (Fig. 5E) similar to those of *L. indicus* in Fig. 3, present on setigers 1–11, followed by paddle-shaped setae.

*Remarks.*—This species was described from male heteronereidid specimens. All specimens are consistent in the pattern of heteronereidid modification. The armature of the other specimen with an everted pharynx in ZMA V. Pol. 538 resembles that of the above-described specimen as follows: area I = 0; II = 3 paragnaths; III = 2 tiny papillae in transverse row; IV = 5 paragnaths; V = 0; VI = 4–5 papillae; VII–VIII = 25 papillae in 2 rows.

On both specimens, the parapodia and setae of the posterior region have been modified dramatically, but the pharyngeal armature, parapodia, and setae of the anterior region closely resemble those of atokous *L. indicus* or *L. nipponicus*. Since *L. indicus* or *L. nipponicus* only differ in the presence of notopodial falcigers on posterior segments, and their heteronereidid specimens have not been reported, it can not be determined, based on available material, whether or not *L. niestraszi* is the male heteroner-

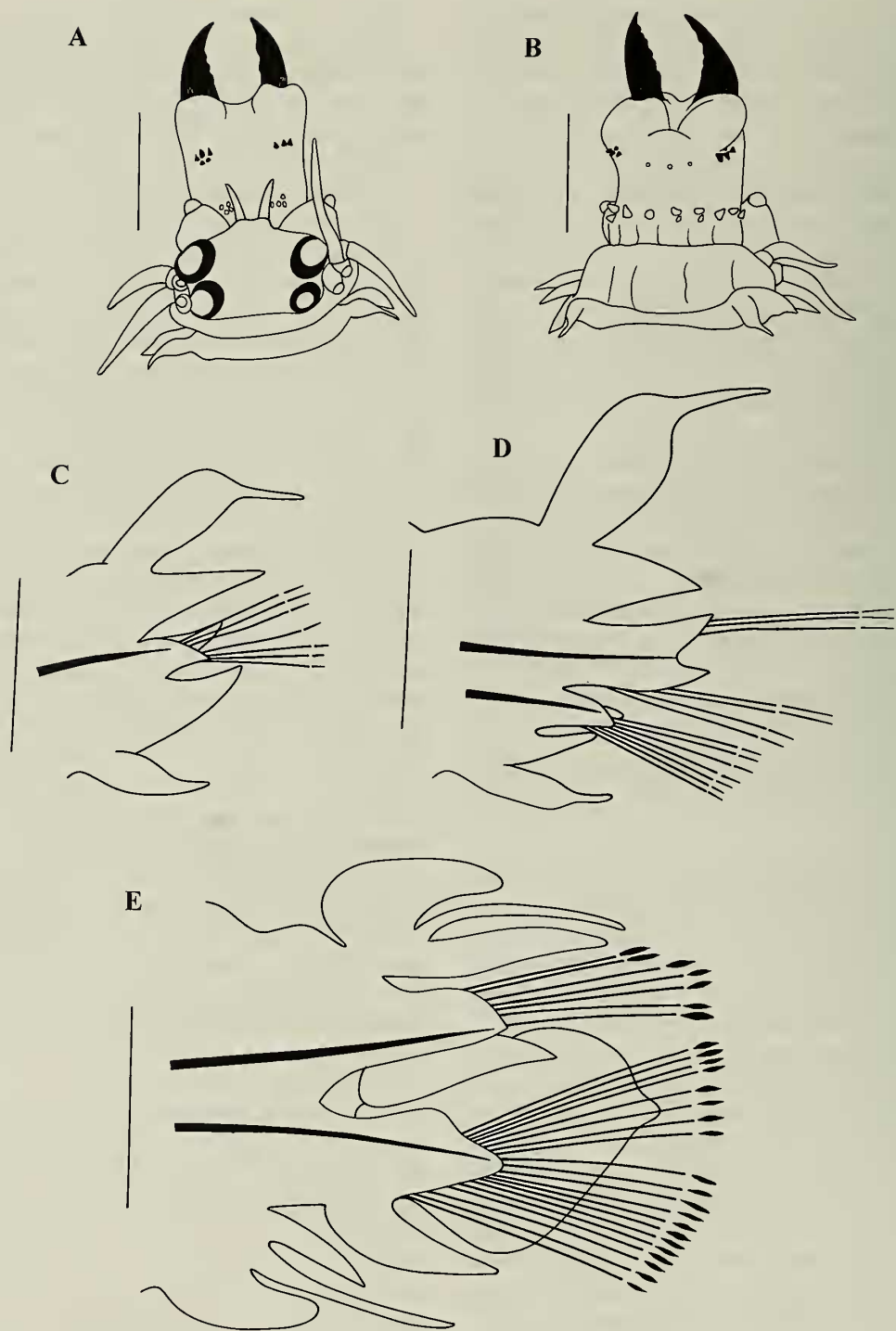


Fig. 4. *Leonnates niestraszi* (ZMA V. Pol. 537). A. Dorsal view of anterior region. B. ventral view of anterior region. C. Anterior view of parapodium 2. D. Anterior view of parapodium 5. E. Anterior view of parapodium 20. (Scale: A-B = 0.5 mm; C-E = 0.25 mm).

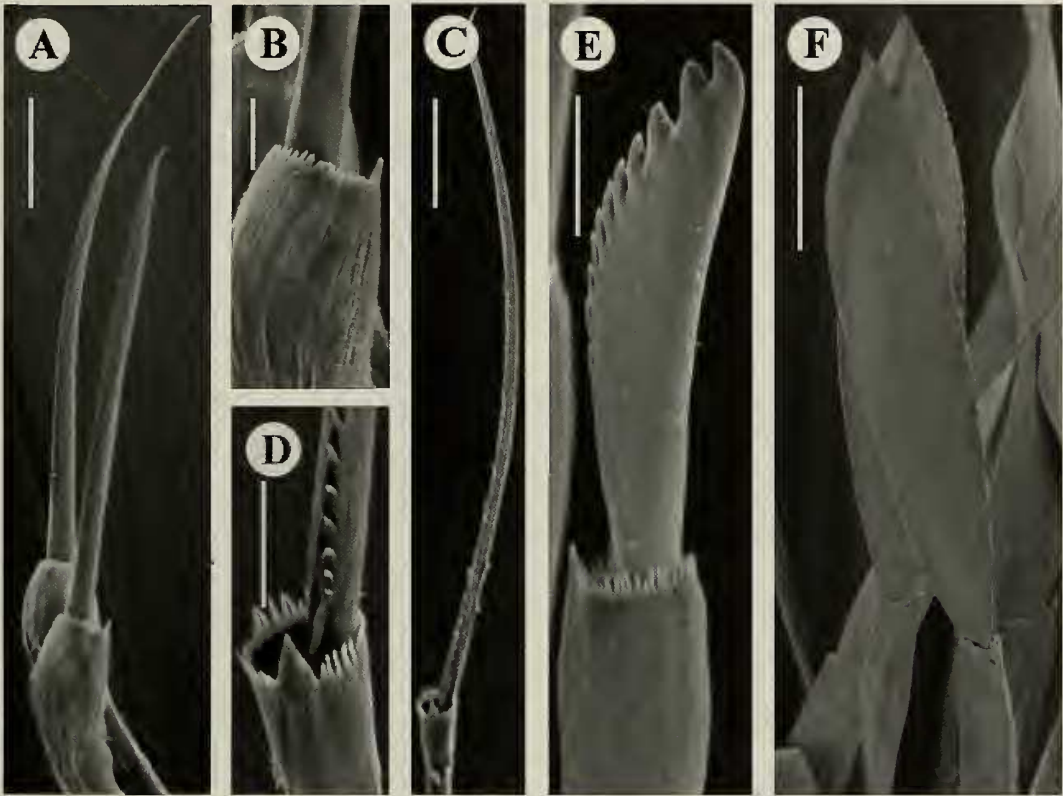


Fig. 5. *Leonnates niestraszi* (ZMA V. Pol. 537). A. Notopodial spinigers from parapodium 5. B. Enlarged end of shaft of one spiniger in A. C. Another notopodial spiniger from parapodium 9. D. Enlarged end of shaft of the spiniger in C. E. Neuropodial falciger from parapodium 5. F. Neuropodial paddle-shaped setae from parapodium 20. (Scale: A = 15  $\mu$ m; B = 5  $\mu$ m; C = 5  $\mu$ m; D = 4  $\mu$ m; E = 10  $\mu$ m; F = 30  $\mu$ m).

eidid form of one of these species. However, characters of specific importance can be found on heteronereidid examples, and additional material may allow for the specific status of *L. niestraszi* to be determined. Furthermore, molecular systematic techniques currently available can possibly be used to clarify the status of this species. Although species status is currently questionable, we proposed that this species be maintained.

*Leonnates decipiens* Fauvel, 1929  
Figs. 6A–D, 7A–B; Table 2

*Leonnates jousseumei* non Gravier. Fauvel  
1927: 427, fig. 106F–H.

*Leonnates decipiens* Fauvel, 1929: 180–

182, fig. 1; 1953: 171–172, fig. 87; Day  
1967: 330, fig. 14.11N–S; Wu et al. 1981:  
65–67, fig. 37; Hartman 1974: 196;  
Hutchings & Reid 1991: 52.

*Leonnates decipiens* var. *manilensis* Pillai,  
1965: 144–148, figs. 13–14.

*Material examined.*—*Leonnates decipiens*: Sungei Baloh, Singapore, 12 Apr 1988, St. 1, dredging, 2 incomplete specimens, one of which female with developing oocytes (NUS 1990: 2260–2270); Qisha, Guangxi Province, China, 11 May 1978 (3 incomplete specimens) (IOCAS 08171); Bailongwei, Guangxi Province, China, 26 May 1978 (1 incomplete specimen) (IOCAS 09112). *L. crinitus* non Hutchings & Reid: Coburg, Trepan Bay, Australia



(11°07'S, 113°58'E), St. CP7/1, 5 m, 15 Sep 1981, coll. Hanley et al., (1 incomplete specimen) (NTM W00388). *L. decipiens* var. *Manilensis*: Government Oyster Farm, Binakayan, Cavite, Manila Bay, Philippines, (2 "paratypes") (BMNH 1965 3.11/12).

*Description*.—The type specimens of *L. decipiens*, collected from the Gulf of Manar and the Suez Canal, were not found in the Muséum National d'Histoire Naturelle, Paris, and they may have been lost. Our description is based on the description by Fauvel (1929) and the characters of the above listed non-type specimens (Table 2).

Prostomium not cleft on the frontal margin. Jaws brownish, smooth. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3–6, in small cluster; III = 4–21; IV = 5–11, in small cluster. Oral ring with soft papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 4–7, in one row. Longest tentacular cirri reaching back 5–6 posterior segments.

Parapodia of first two setigers uniramous, without notosetae (Fig. 6A). In other anterior segments, neuropodial postsetal ligule with finger-like protrusion on upper tip (Fig. 6B); protrusion reduced along body and absent posteriorly from middle of body (Fig. 6C, D). Neuropodial ventral ligule in middle and posterior regions long and pointing ventrally. Dorsal cirrus shorter than dorsal notopodial ligule; ventral cirrus shorter than dorsal cirrus.

Notopodia with homogomph spinigers throughout. Spinigers identical to those of *L. indicus*, except shaft with large tooth deeply cleft on both sides and with circular fringe of slender teeth (Fig. 7A). Neuropodia with homogomph spinigers and heterogomph falcigers (Fig. 7B). Spinigers similar to notosetae, present throughout, accompanied by falcigers on middle neuropodia. Falcigers with short blade carrying straight terminal projection and fringe of smaller teeth on cutting edge; end of shaft with large tooth extending beyond circular fringe of smaller teeth (Fig. 7B); Falcigers

Table 2.—Diagnostic characteristics of *Leonnates decipiens*. Numbers of processes on the left side and right side of areas II and IV are separated by a slash. In BMNH 1965.3 11/12 the number of falcigers and their occurrence in the exact neuropodia in the middle region were not examined. Numbers following original catalogue numbers are added to distinguish the specimens in the same lot.

Specimen cat. no.	No. of setigers	Size (mm)	Paragnaths on					Papillae on		Neuropodial falciger(s) on setigers	Neuropodial falcigers	
			I	II	III	IV	V	VI	VII–VIII		upper fascicle	lower fascicle
NUS 1990.2260– 2270.1	10*	2 × 5	0	6/5	21	8/8	0	1	5 in 1 row	N/A	N/A	N/A
NUS 1990.2260– 2270.2	58*	1.5 × 16	0	5/6	13	8/10	0	1	6 in 1 row	15–36	1–2	2–5
BMNH 1965 3.11/12	70	1 × 12	0	3/4	3	6/5	0	1	0	Not examined	Not examined	Not examined
NTM W00388	53*	1.9 × 15	0	6/5	11	6/7	0	1	5 in 1 row	13–43	1–2	2–7
IOCAS 08171.1	23*	2 × 11	0	4/5	7	5/7	0	1	7 in 1 row	14–23	1–2	4–6
IOCAS 08171.2	27*	2.1 × 12	0	5/5	11	6/6	0	1	6 in 1 row	13–27	1–3	2–8
IOCAS 08171.3	29*	1.9 × 18	0	3/5	7	8/11	0	1	4 in 1 row	15–39	1–2	2–7
IOCAS 9112	24*	0.6 × 13	0	5/5	4	5/5	0	1	5 in 1 row	13–24	1–2	2–4

\* incomplete.

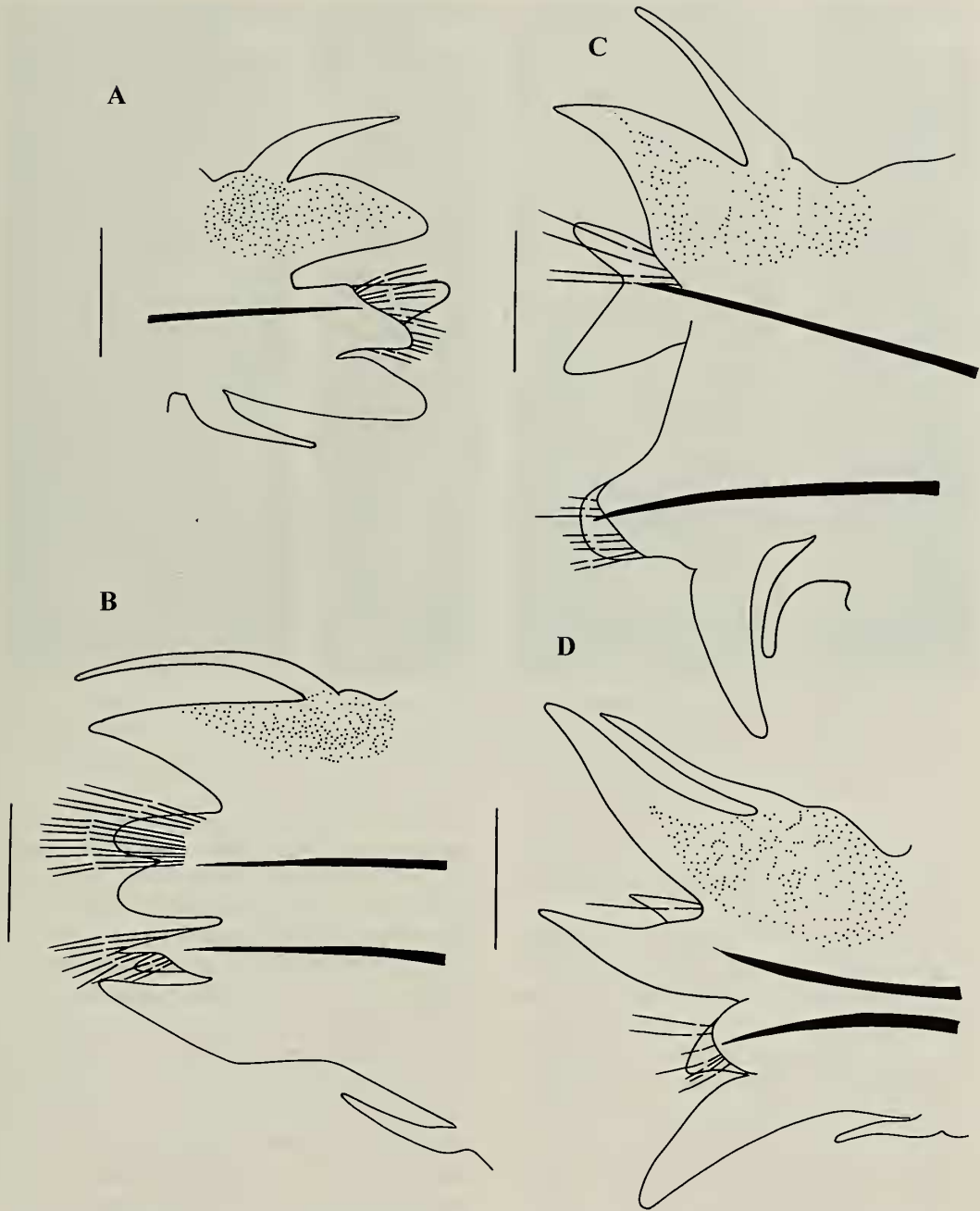


Fig. 6. *Leonnates decipiens* (NUS 1990.2260–2270). A. Anterior view of parapodium 2. B. Posterior view of parapodium 10. C. Posterior view of parapodium 20. D. Posterior view of parapodium 37. (Scale: A–D = 0.15 mm).

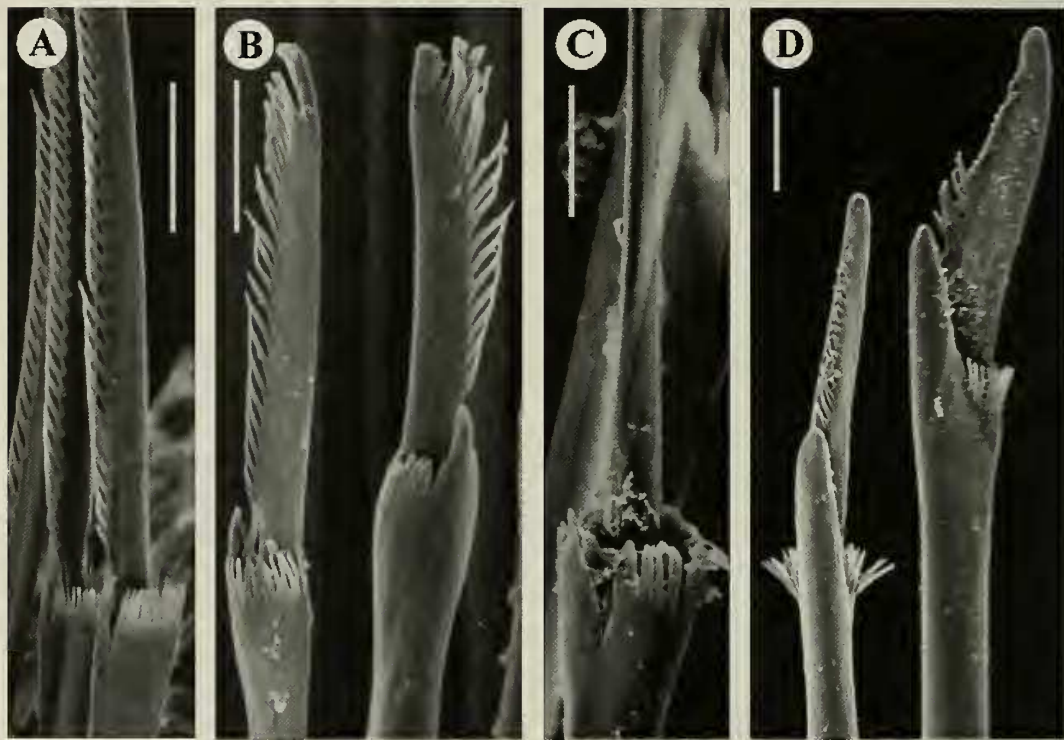


Fig. 7. *Leonnates decipiens* (NUS 1990.2260–2270). A. Notopodial spinigers from parapodium 20. B. Neuropodial falcigers from parapodium 20, the terminal projection of the seta on the right is broken off. *Leonnates simplex* (BMNH 1941.4.4.2). C. Notopodial spiniger from parapodium 20. D. Neuropodial falcigers from parapodium 20. (Scale: A = 10  $\mu$ m; B = 10  $\mu$ m; C = 7.5  $\mu$ m; D = 10  $\mu$ m).

present from setiger 13–15 to setiger 23–43, numbering 1–2 in upper fascicle and 2–7 in lower fascicle (Table 2).

**Remarks.**—Fauvel (1929) differentiated *L. decipiens* from *L. jousseaumei* in that his new species had fewer processes on the pharynx, especially the oral ring, a different shape of falciger, and a different pattern of occurrence of falcigers along the body. The different pharyngeal armature is as follows: area VI = a large papilla; VII–VIII = 7–8 smaller papillae, sometimes more or less absent. The falcigers of *L. decipiens* were described with spinuous convex blade and blunt truncated tip, and occurred only on the neuropodia of the middle region. The non-type specimens examined, although not from the type locality, share the above characters. Apart from the differences in the pharyngeal processes and the shape and pattern of occurrence of the falcigers, *L. de-*

*cipiens* also differs from *L. indicus* in the shape of parapodia: in the anterior setigers, the neuropodial postsetal ligule has a prominent finger-like protrusion on the upper tip (Fig. 6B), absent on *L. indicus*; in the middle and posterior setigers, the neuropodial postsetal ligules greatly reduced while the ventral neuropodial ligule is much longer than the neuropodial acicular lobe and postsetal ligule (Fig. 6C, D), whereas in *L. indicus* the neuropodial postsetal ligule is similar along the body, and the ventral neuropodial ligule is of similar length to the neuropodial acicular lobe and postsetal ligule. The long and often ventrally pointed ventral neuropodial ligule can be seen in the drawings of Fauvel (1929, fig. 1B; 1953, fig. 87B), but the reduction of the neuropodial postsetal ligule is not shown in his drawings of posterior parapodia (Fauvel 1929, fig. 1B; 1953, fig. 87B).



Pillai (1965) established the nomenclaturally invalid (Article 16, International Commission on Zoological Nomenclature, 1985: "A scientific name proposed expressly as the name of a 'variety' or 'form' after 1960 is infrasubspecific and excluded from zoological nomenclature") *L. decipiens* var. *manilensis* based on the occurrence of fewer (4 instead of 7–8) papillae on area VII–VIII of the proboscis and that these papillae are larger than the paragnaths of the maxillary ring. A "holotype" and two "paratypes" of *L. decipiens* var. *manilensis* were collected from an oyster farm in Manila. The "holotype" (University of Ceylon, RTS 21) was not available for examination. Of the two "paratypes", the one with everted pharynx has no obvious papillae on area VII–VIII (Table 2), and we were not authorized to dissect the pharynx of the other. Fauvel (1929) also reported a lack of papillae on pharyngeal areas VII–VIII of some of his specimens, and his description of the papillae on this area, however, can be interpreted to say that they are much or slightly smaller than those on area VI. On the non-type *L. decipiens* specimens we examined (Table 2), the number of papillae on areas VII–VIII varies from 5 to 6, slightly more than on the "holotype" of *L. decipiens* var. *manilensis*; they are of similar size to the papilla on area VI, but larger than the paragnaths on the maxillary ring. The pharyngeal areas II, III, and IV of this *L. decipiens* var. *manilensis* specimen have paragnaths comparable to those of other *L. decipiens* specimens examined, but they have fewer paragnaths than on the corresponding areas of the *L. decipiens* var. *manilensis* "holotype". The long and often ventrally pointed ventral neuropodial ligule can be seen in the original drawings of Pillai (1965, fig. 14B–D). Pillai also noted that the neuropodial postsetal ligule is lacking in the middle setigers (Fig. 14B, C, in Pillai 1965), but it reappears on posterior setigers as a long digit (Fig. 14D, in Pillai 1965). This structure is absent from the posterior segments of all the specimens we exam-

ined. The characters that Pillai (1965) used to support the establishment of *L. decipiens* var. *manilensis* are common among specimens of *L. decipiens*, and our opinion is that Pillai's are perfectly good specimens of *L. decipiens* Fauvel.

*Habitat*.—Fauvel (1927, 1929, 1953), Day (1967) and Hartman (1974) did not give habitat information for their material. The specimens described as *L. decipiens* var. *manilensis* were collected from an oyster farm (Pillai 1965). A male heteronereid, with significantly modified parapodia, was collected from a pearl oyster farm (Wu et al. 1981). Other specimens described in Wu et al. (1981) were collected from 0–40 m in an estuarine, sandy mud environment. Those in Hutchings & Reid (1991) were found among coral rubble and sandy substrata.

*Distribution*.—Congo, Senegal, and Mozambique, Africa; Northern Territory, Australia; Gulf of Mannar; Suez Canal; Sri Lanka; Guangdong & Guangxi Provinces, China.

*Leonnates insolitus* Gravier & Dantan,  
1934

*Leonnates insolita* Gravier & Dantan, 1934:  
37–135, figs. 4–8.

*Material examined*.—None. The original description was based on a heteronereidid collected from the surface water during the night of 29 Jun 1927 in South Viet Nam. The author did not note where the type specimen was deposited. The polychaete curators of the Institute of Oceanography, Nha Trang, and Muséum National d'Histoire Naturelle, Paris found no record of this species in their catalogues.

*Description*.—Pharyngeal jaws with 6–7 denticles; maxillary ring with paragnaths arranged as follows: area I = 0; II = 3–5; III = 0; IV = 3; oral ring with soft papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 2 rows.

Body divided into two regions: slightly modified anterior region consisting of 9 se-

tigers and highly modified posterior region consisting of remaining.

Anterior region, parapodia after first 2 biramous with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule conical, similar to notopodial acicular ligule. Dorsal cirrus swollen at base. Neuropodial postsetal ligule small, slightly larger than presetal acicular ligule; shorter than notopodial ligules. Ventral neuropodial ligule slightly longer than neuropodial lobe and ligule. Ventral cirrus short with slightly swollen base (Gravier & Dantan, fig. 5, who stated that ventral cirrus was broken off).

Parapodia from setiger 10 greatly modified with thin accessory flaps at base of dorsal cirrus, on postsetal lobe of neuropodial acicular lobe, and at base of ventral cirrus. Dorsal cirrus and ventral cirrus slender. Dorsal cirrus extending beyond dorsal notopodial ligule.

Notopodia of anterior region each with aciculum, but without setae. Neuropodia each with aciculum and few homogomph spinigers. Setae of posterior region of both notopodia and neuropodia paddle-shaped.

Pygidium without rosette of papillae.

*Remarks.*—Based on the shape of pygidium, Gravier & Danton (1934) suggested their material was a female. They did not report whether oocytes were present in the coelom. Atokous specimens of *L. insolitus* have not been reported, and the extent to which the heteronereidids differ from them is unknown. The pharyngeal armature of this species resembles that of *L. persicus*, but anterior parapodia differ from those of all other *Leonnates* species in lacking setae in notopodia. This lack of setae in anterior notopodia is probably a result of the heteronereidid modification and may not be found on atokous specimen of this species. Currently, the specific status is indeterminate. However, this species is maintained in *Leonnates* in anticipation that additional material from the type locality will allow

for more definitive determination of its status.

*Leonnates simplex* Monroe, 1939

Figs. 7C–D, 8A

*Leonnates simplex* Monroe, 1939: 403–405, text-fig. 305.

*Material examined.*—Holotype: from Aldabra Island, Indian Ocean (BMNH 1941.4.4.2).

*Description.*—Holotype complete, except pygidium damaged with anal cirri missing, 2.2 by 55 mm, 110 setigers. Animal colour greyish, with darker parapodial glands at base of dorsal notopodial ligule. Prostomium pentagonal, not cleft on frontal margin. Antennae approximately half as long as palps. Two pairs of eyes equal-sized, black. Palps long, cylindrical, with small palpostyles. Peristomium with slender tentacular cirri, the longest reaching setiger 5.

Pharynx everted with jaws brownish, with dentate cutting edge. Maxillary ring with paragnaths arranged as follows: area I = 2; II = 9, each side in small cluster; III = 15 left, 16 right, each in small cluster; IV = 20 left, 23 right, each in cluster. Oral ring with soft papillae and paragnaths arranged as follows: area V = 3 papillae, in triangle; VI = transverse row of numerous minute paragnaths, exact number not determinable; VII–VIII = 21 papillae, in 2 rows.

Parapodia of first 2 setigers uniramous without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal lobe, and ventral neuropodial ligule. Dorsal notopodial ligule conical, approximately as long as dorsal cirrus. Neuropodial presetal acicular lobe of similar size to neuropodial postsetal lobe, smaller than dorsal notopodial ligule. Ventral neuropodial ligule conical, slightly longer than neuropodial presetal acicular lobe. Ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial infra-acicular ligule, neuropodial presetal acicular

lobe, neuropodial postsetal acicular lobe, and ventral neuropodial ligule (Fig. 8A). Dorsal notopodial ligule blunt, with yellowish glandular region at base of dorsal cirrus; ligule becoming slightly smaller on posterior setigers but shape remaining similar. Notopodial infra-acicular ligule similar to dorsal notopodial ligule in shape and size. Dorsal cirrus subulate, approximately as long as dorsal notopodial ligule on anterior setigers, extending slightly beyond dorsal notopodial ligule on posterior setigers. Neuropodial presetal acicular lobe smaller than notopodial ligule, blunt with short, rounded postsetal lobe. Ventral neuropodial ligule smaller than but approximately as long as neuropodial presetal acicular lobe. Ventral cirrus subulate, about as thick but shorter than dorsal cirrus.

Notopodia with 1–3 homogomph spinigers (Fig. 7C); each with slender blade 100–130  $\mu\text{m}$  long, fringed with small teeth on cutting edge; end of shaft with large tooth surrounded by fringe of smaller teeth, all of similar length; both sides of large tooth with split cutting into shaft (Fig. 7C). Neuropodia with spinigers similar to notopodial spinigers and heterogomph falcigers, present throughout, the latter located in the lower position of fascicle. Falcigers with short triangular blade, about 35  $\mu\text{m}$  long, fringed with small teeth on cutting edge; large tooth at end of the shaft facing cutting edge of blade, much longer than surrounding fringe of smaller teeth (Fig. 7D).

Gender indeterminable.

*Remarks.*—Monro (1939) described this species as differing from *L. indicus* and *L. decipiens* in having only two notopodial ligules, heterogomph falcigers with very short blades, and a quite different pharyngeal armature. The original description is detailed and accompanied by drawings of the head region, parapodia and setae. However, the pharyngeal armature on area VI, originally described as papillae, are sclerotized structures, which should be considered as paragnaths. The occurrence of par-

agnaths on this area has not been reported in any other *Leonnates* species.

*Habitat.*—Not mentioned in the original description.

*Distribution.*—Aldabra Islands, Indian Ocean.

*Leonnates persicus* Wesenberg-Lund, 1949

Figs. 8B–C, 9A–C, 10A–E, 11A–D;  
Table 3

*Leonnates persica* Wesenberg-Lund, 1949: 275–277, figs. 11–12; Day 1967: 328–329, fig. 14.11. G–M; Wu et al. 1981: 68–69, figs. 39–40.

*Material examined.*—2 miles West of Mujgam, Persian Gulf (26°57'N, 53°26'E), 10 Apr 1938 (holotype, ZMUC). Off East Sha Chau, Hong Kong (22°17'N, 113°52'E), Feb 1999 (2 complete specimens) (HKUST W0006–W0007) (1 incomplete specimen) (HKUST W0013); Feb 1998 (5 incomplete specimens) (HKUST W0008–W0012).

*Description of holotype.*—The original description, based on an anterior fragment with 30 setigers, is incomplete.

Animal colour cream with darker pigmentation at base of dorsal cirrus and dorsal notopodial ligule. Prostomium pentagonal with cleft on frontal margin. Two pairs of black eyes, arranged trapezoidally; anterior pair slightly larger. Palps thick, cylindrical, each with small palpostyle. Antennae digitiform, approximately as long as palps. Peristomial cirri slender and tapering; dorsal most pair missing; remaining longest reaching back to setiger 5.

Pharynx everted with jaws brownish, smooth. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3 left, 2 right; III = 0; IV = 3. Oral ring with papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 29, in 3 irregular rows.

Parapodia of first 2 setigers with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule asetigerous, conical, with basal



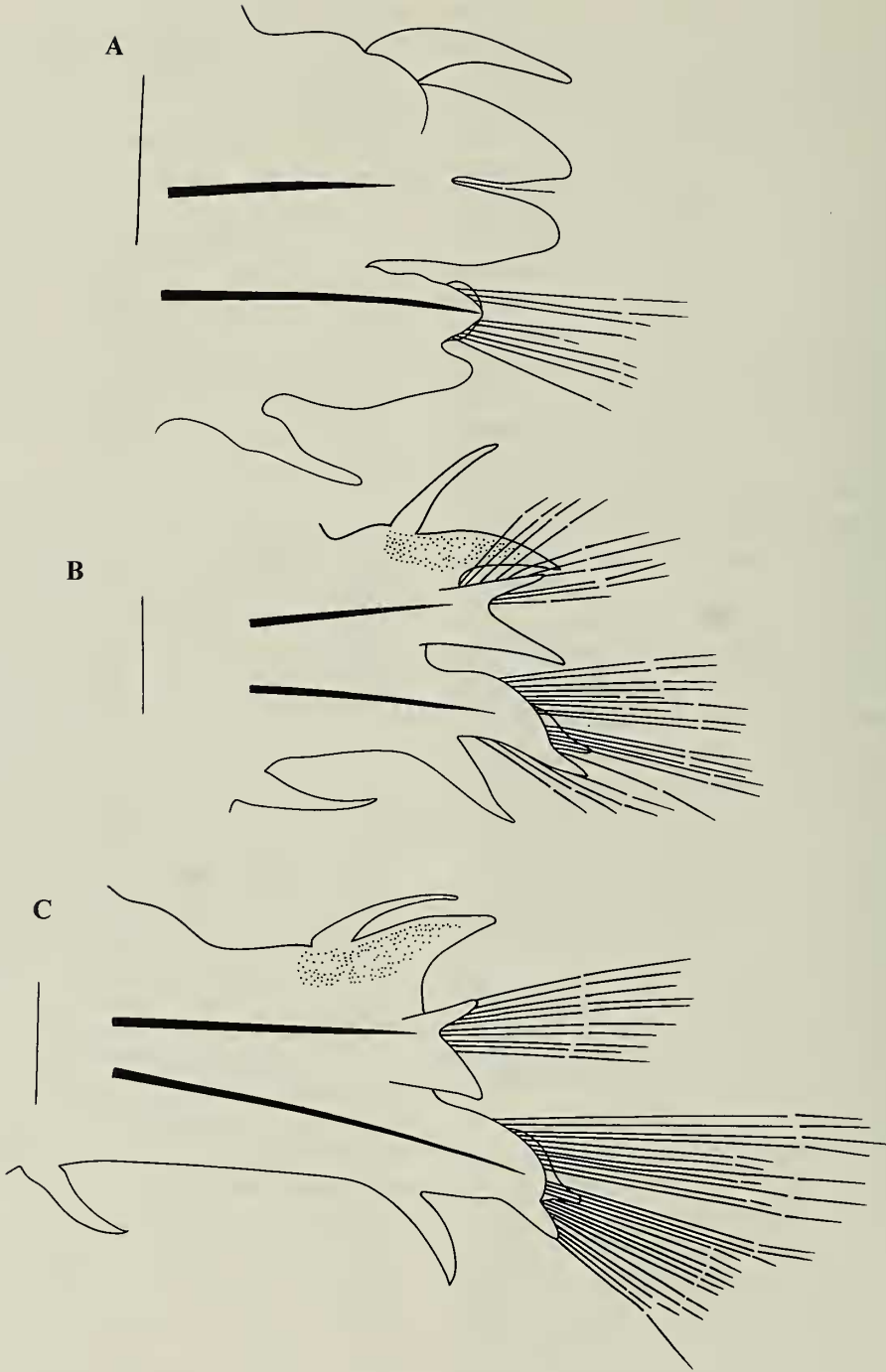


Fig. 8. *Leonnates simplex* (BMNH 1941.4.4.2). A. Anterior view of parapodium 20. B–C. *Leonnates persicus* (Holotype ZMUC). B. Anterior view of parapodium 3. C. Anterior view of parapodium 20. (Scale: A–C = 0.25 mm).

swelling. Dorsal cirrus subulate, slightly shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule conical, slightly longer than postsetal ligule. Neuropodial ventral ligule conical, of similar length to postsetal ligule. Ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 8B, C). Dorsal notopodial ligule large, conical, swollen at base, with glandular region at upper margin, becoming slightly larger on middle setigers with shape unchanged. Notopodial supra-acicular ligule conical, similar to but smaller than infra-acicular ligule. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. In anterior segments, neuropodial presetal acicular ligule shorter than postsetal ligule, with digit protruding from lower frontal tip (Fig. 8B). In middle neuropodia, presetal ligule and postsetal ligule similar in shape and size (Fig. 8C). Ventral neuropodial ligule conical, smaller than, but of similar length to neuropodial presetal acicular ligule. Ventral cirrus subulate, same thickness as dorsal cirrus but shorter.

Notopodia with homogomph spinigers throughout, each with slender blade fringed with small teeth on cutting edge. Large tooth at end of shaft surrounded by fringe of slender teeth of similar length, with split cutting into shaft on both sides of large tooth (Fig. 9A, B). Neuropodia with two kinds of setae: homogomph spinigers and homogomph falcigers. Spinigers similar to those on notopodia, present throughout fragment, fewer on middle neuropodia where accompanied by falcigers. Falcigers present on neuropodia from setiger 10 to end of fragment (setiger 30), numbering 3–6 in supra-acicular fascicle and 4–16 in infra-acicular fascicle, blades with straight terminal projection, fringed on cutting edge. Tooth at end of shaft fringed by circular

slender teeth of similar length; split cutting into the shaft on both sides of large tooth (Fig. 9C).

Gender of holotype, as well as most of our material, indeterminable. Specimen HKUST W0013 with developing oocytes diameter 60–80  $\mu\text{m}$ , without heteronereidid modification. Female with mature oocytes diameter 100  $\mu\text{m}$ , without heteronereidid modification, and male heteronereidid with modified eyes, parapodia and setae reported by Wu et al. (1981).

*Remarks.*—Although the original description is quite detailed, it is incomplete as only an anterior fragment was available. The parapodia and setae of our material match well with those of the holotype (Figs. 9A–C, 11, present study; fig. 12, Wesenberg-Lund 1949). In the holotype, as well as all other material described in previous studies (Day 1967, Wu et al. 1981), pharyngeal areas I and III are devoid of paragnaths. Slight variation in the number of paragnaths on areas I and III (0–1 on area I, 0–3 on area III) were found in our specimens collected from the same locality (Fig. 10, Table 3), but we believe this minor variation is intraspecific; some of these specimens have the exact numbers of paragnaths as those occurring on the corresponding areas of the holotype. Greater variation in numbers of soft papillae was found on area VII–VIII: area VII–VIII has 3–4 rows of papillae according to Day (1967) and Wu et al. (1981). The number of rows of papillae on areas VII–VIII of our specimens varies from 2 to 3–4. A correlation between body size and numbers of papillae on area VII–VIII shows this variation is likely to be due to differences in body size: larger individuals usually have more papillae than smaller individuals [ $Y = 6.16X + 6.48$ ,  $Y$  = number of papillae on areas VII–VIII,  $X$  = Body width (mm),  $n = 9$ ,  $r = 0.949$ ].

The left parapodium 20 from the holotype, which contained both falcigers and spinigers, was the only parapodium of the middle region that was authorized to dissect for SEM. The line drawing and observa-

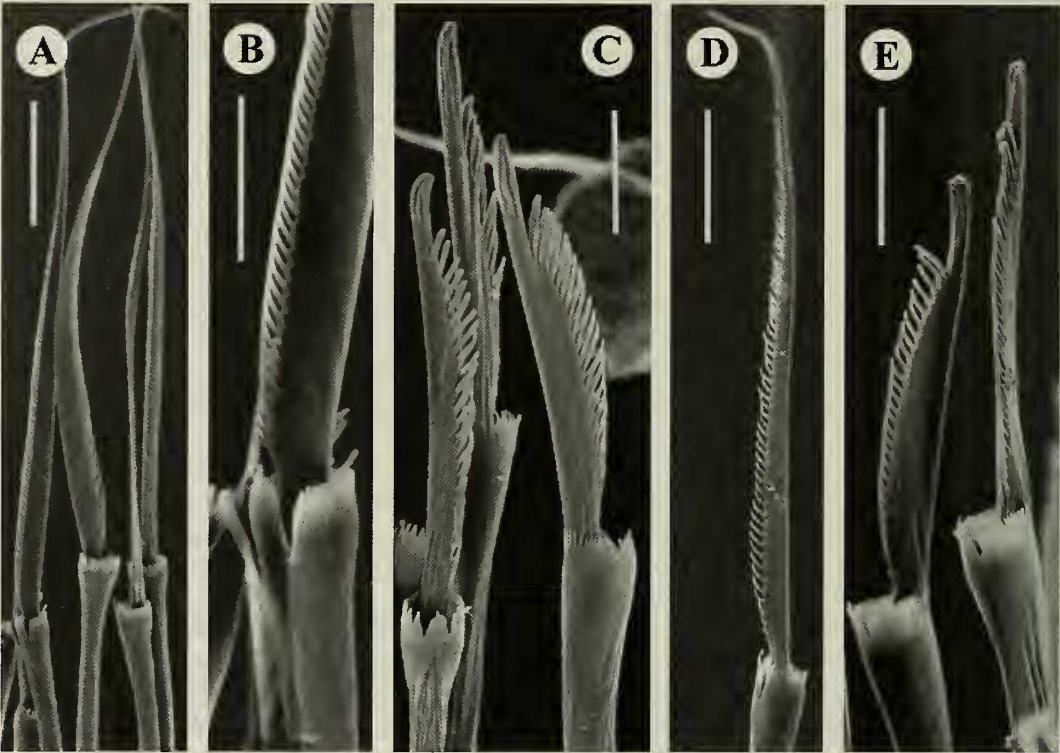


Fig. 9. *Leonnates persicus* (HKUST W0006). A. Notopodial spinigers from parapodium 20. B. Enlarged end of shaft of one of the spinigers in A. C. Neuropodial falcigers from parapodium 20. *Leonnates stephensoni* (AM W10258). D. Notopodial spiniger from parapodium 2. E. neuropodial falciger from parapodium 20. (Scale: A = 25  $\mu$ m; B = 10  $\mu$ m; C = 10  $\mu$ m; D = 15  $\mu$ m; E = 15  $\mu$ m).

tions using dissecting and compound microscopes were successful, but unfortunately, the setae were broken during preparation for SEM. Since substantial evidence indicates that our specimens are *L. persicus*, a parapodium from the same body region of HKUST W0006 was used for SEM.

Our specimens (Table 3) have provided supplemental information on the posterior region of this species. The notopodial supra-acicular ligule gradually diminishes along the body but remains distinct on posterior region (Fig. 9). The notopodial infra-acicular ligule becomes slightly smaller on posterior region. In anterior segments, the neuropodial presetal acicular ligule is blunt, shorter than postsetal ligule, with a digit protruding from the lower frontal margin. In middle and posterior parapodia, the neu-

ropodia presetal ligule and postsetal ligule are of similar shape and size. The pygidium has two anal cirri that extend for a length equivalent to approximately 15 posterior setigers. Neuropodial falcigers disappear from posterior segments.

*Habitat.*—The holotype was collected from 20 m, in clay with little sand, co-existing with *Pseudeurythoe hirsuta* Wesenberg-Lund, 1949. Our specimens were collected by a grab from 5–11 m depths, in clay with silt; salinity at the site fluctuated on a seasonal cycle, reaching 19.3 ppt during the summer and 32.5 ppt during the winter. The material in Wu et al. (1981) was collected from a variety of localities along the Chinese coast (fig. 18 in Wu et al. 1981) from 1.5–58 m depths, in sandy mud or clay, co-existing with *Venerupis* sp., *Am-*



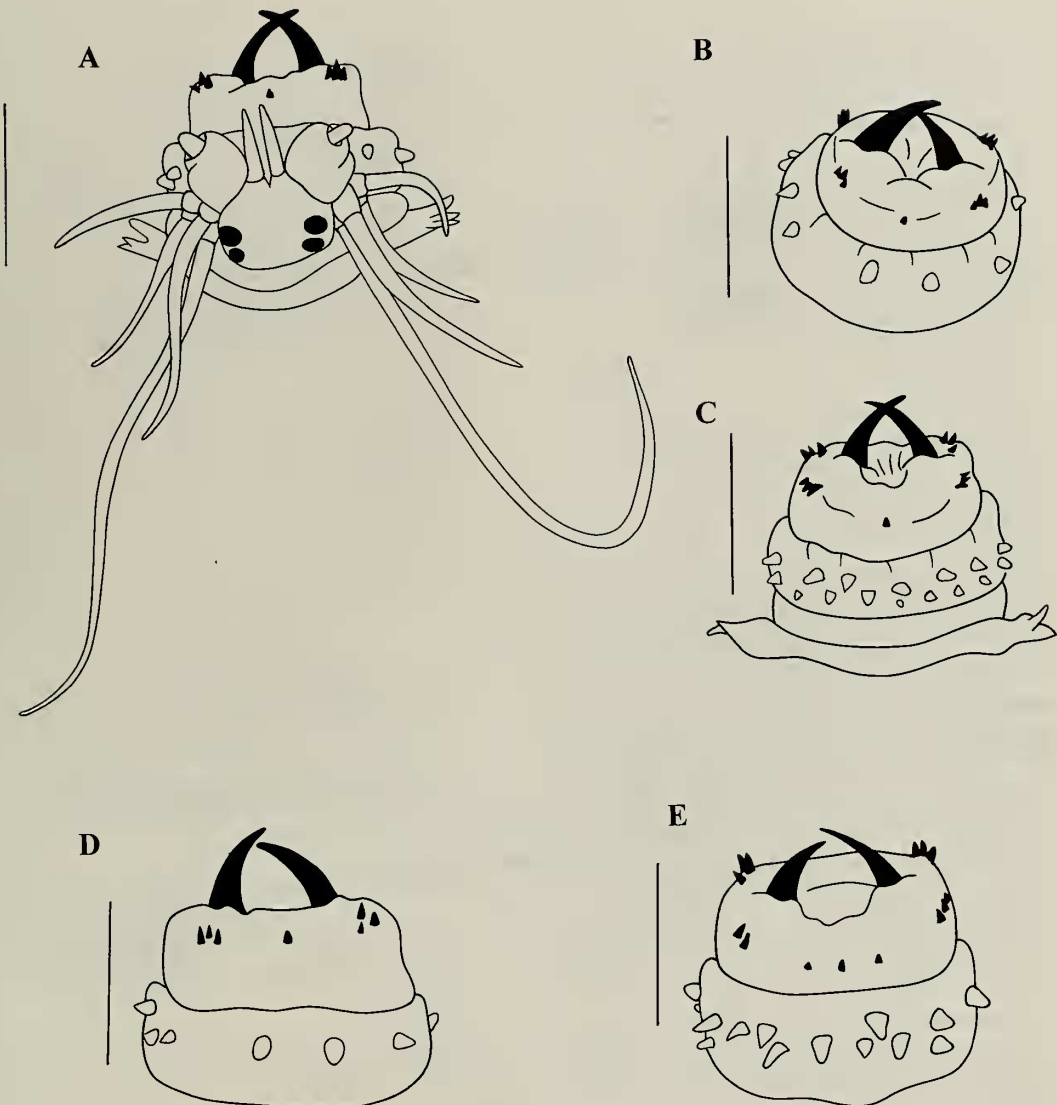


Fig. 10. *Leonnates persicus* (A–C: HKUST W006; D–E: HKUST W008). A. Dorsal view of anterior region. B. Dorsal view of pharynx. C. Ventral view of anterior region. D. Dorsal view of pharynx. E. Ventral view of pharynx. (Scale: A–E = 0.5 mm).

*phiura vadicola* Matsumoto, *Loimia medusa* (Savigny) and *Eudistylia vancouveri* (Kinberg).

*Distribution*.—South Africa; Persian Gulf; China.

*Leonnates stephensoni* Rullier, 1965  
Figs. 9D–E, 12

*Leonnates stephensoni* Rullier, 1965: 174–177, fig. 4A–I; Hutchings & Murray

1984: 36–37, fig. 11; Hutchings & Reid 1991: 53–54.

*Leonnates persicus* non Wesenberg-Lund.  
Gallardo 1967: 64, pl. 14, figs. 1–4.

*Material examined*.—Calliope River, Queensland (23°55'S, 151°10'E), coll. Saenger, May 1976 (4 specimens) (AM W13513); Auckland Creek, Queensland (23°50'S, 151°16'E), 9–12 Feb 1976, coll. Saenger (1 specimen) (AM W10258).

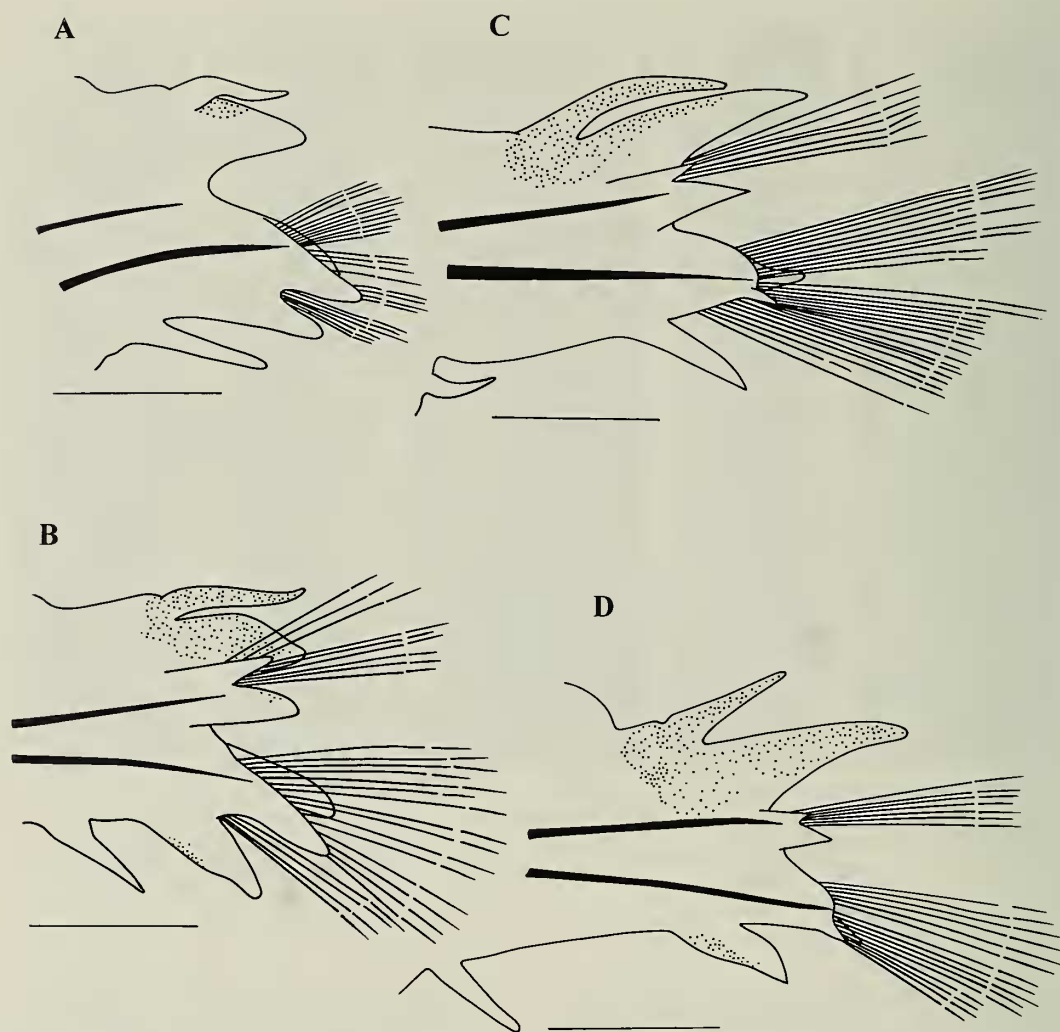


Fig. 11. *Leonnates persicus* (HKUST W0006). A. Anterior view of parapodium 2. B. Anterior view of parapodium 3. C. Anterior view of parapodium 20. D. Anterior view of parapodium 40. (Scale: A–D = 0.2 mm).

**Description.**—The holotype (AM W3790), an anterior fragment of 27 setigers from Moreton Bay, Queensland (27°25'S, 151°10'E), was not available for examination. All specimens examined were also from Queensland and are incomplete. The longest fragment (AM W10258, 19 mm long with 34 setigers), is the example chosen for description.

Animal colour cream with glandular region at base of dorsal cirrus. Prostomium pentagonal, cleft on frontal margin. Anten-

nae barely reaching joint between palpopore and palpostyle. Two pairs of eyes in trapezoidal arrangement, anterior pair slightly larger. Peristomium with tentacular cirri, longest reaching back to setiger 10.

Pharynx with slightly denticulate jaws. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3 left, 1 right; III = 0, IV = 3. Oral ring with papillae arranged as follows: V = 1; VI–VIII = 61 in 3–4 irregular rows.

Parapodia of first 2 setigers with dorsal

Table 3.—Diagnostic characteristics of *Leonnates persicus*. Numbers of processes on the left side and right side of pharyngeal areas II and IV are separated by a slash.

Specimen cat. no.	Size (mm)	No. of setigers	Paragnath(s) on area				Papillae on area			Neuropodial falcigers on setigers	Neuropodial falcigers	
			I	II	III	IV	V	VI	VII–VIII		upper fascicle	lower fascicle
ZMUC**	4.3 × 14	30*	0	3/2	0	3/3	0	1	29 in 3 rows	10–30	3–6	4–16
HKUST W0006	1.5 × 15	81	1	3/3	1	3/3	0	1	18 in 2 rows	9–31	2–4	3–14
HKUST W0007	2.1 × 18	76	0	3/2	0	3/3	0	1	19 in 2 rows	9–31	2–5	2–16
HKUST W0008	2.1 × 11	45*	1	3/3	3	2/3	0	1	19 in 2 rows	8–30	1–3	3–13
HKUST W0009	2 × 13.5	56*	0	3/3	1	3/3	0	1	19 in 2 rows	10–29	2–4	2–12
HKUST W0010	2.4 × 19.4	55*	1	3/3	2	3/3	0	1	22 in 2 rows	11–33	2–4	2–14
HKUST W0011	2.6 × 20.5	39*	0	2/3	2	2/3	0	1	19 in 2 rows	11–34	2–7	6–20
HKUST W0012	2.6 × 3.3	40*	1	4/3	3	3/4	0	1	24 in 2 rows	9–34	2–6	2–14
HKUST W0013	5.2 × 17.5	18*	0	2/4	0	3/3	0	1	42 in 3–4 rows	10–18	6–10	9–18

\* incomplete; \*\* holotype, without catalogue number.

notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 12A). Dorsal notopodial ligule asetigerous, large, conical. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule dorsolaterally pointed. Neuropodial postsetal ligule ventrolaterally pointed. Ventral neuropodial ligule conical, similar to neuropodial acicular ligules. Ventral cirrus subulate, about as long as dorsal cirrus.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 12B, C). Dorsal notopodial ligule large, conical, longer than notopodial presetal acicular ligule. Notopodial supra-acicular ligule slightly smaller than infra-acicular ligule (Fig. 12A, B). Notopodial supra-acicular ligule gradually diminishing along body, but remaining distinct on setiger 34 (last setiger of fragment); infra-acicular ligule similar along body. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule projecting ventrolaterally; neuropodial postsetal ligule projecting horizontally; presetal acicular ligule diminishing posteriorly but present on posterior segments of fragment as small, ventrally located cone. Ventral neuropodial ligule smaller than, but approximately as long as neuropodial postsetal ligule. Ventral cirrus subulate, slightly shorter than dorsal cirrus.

Notosetae all homogomph spinigers, each with slender blade fringed on cutting edge; end of shaft with tooth as long as surrounding fringe of slender teeth (Fig. 9D). Neurosetae homogomph spinigers and homogomph falcigers. Spinigers similar to those on notopodia, present throughout. Falciger present on setigers 9–34 of fragment, numbering 6–8 in supra-acicular fascicle and 9–15 in infra-acicular fascicle; blades with straight terminal projection and fringed cutting edge; shaft ending with



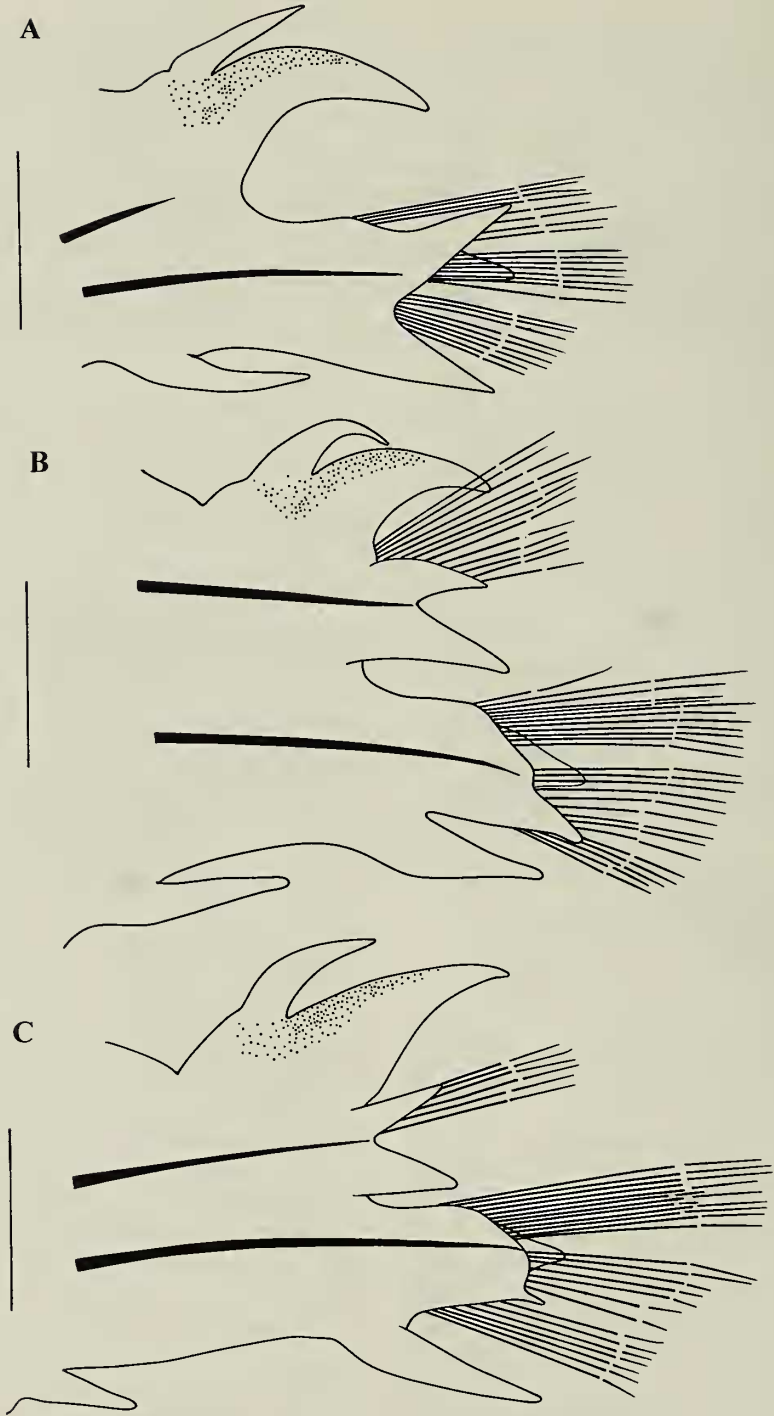


Fig. 12. *Leonnates stephensoni* (AM W10258). A. Anterior view of parapodium 2. B. Anterior view of parapodium 6. C. Anterior view of parapodium 20. (Scale: A-C = 0.3 mm).

tooth extending to the tip of surrounding fringe of slender teeth (Fig. 9E).

Female with developing oocytes diameter 55–70  $\mu\text{m}$ .

*Remarks.*—According to Rullier (1965), *L. stephensoni* differs from *L. persicus* in having a darkened glandular region on the parapodia, three papillae on area V of proboscis, greater attenuation of falciger blades, a straight tip of falciger blades (rather than a broadly truncated tip) and falcigers with a perfectly homogomph articulation, rather than being slightly heterogomph. Our examination of the holotype of *L. persicus* reveals that it also has darkened glandular regions on the parapodia (Fig. 8B, C), not reported in the original description (Wesenberg-Lund 1949). The non-type *L. stephensoni* specimens also have papillae on the oral ring, but the exact number varies from the 3 reported in the original description: i.e., 1 to 3 on area V, and there are 2–4 continuous rows of papillae on area VI–VIII. SEM shows that the falcigers of *L. stephensoni* and *L. persicus* are very similar in having a homogomph articulation, a straight tip and a fringed cutting edge (Fig. 9C, E). The original description of *L. stephensoni*, which states that the falciger blades are more attenuated than those of *L. persicus*, and that those of *L. persicus* have a slightly heterogomph articulation (Rullier 1965) are incorrect.

*Leonnates stephensoni* appears to differ from *L. persicus* in having one or more papillae on area V and continuous rows of papillae on areas VI–VIII. Gallardo (1967) reported *L. persicus* from Nha Trang, Viet Nam. His description, however, shows 1 papilla on area V and 40–50 papillae on areas VII–VIII, so his specimen likely belongs to *L. stephensoni*. A specimen (AM W202003), identified as *L. stephensoni* by Hutchings & Reid (1991), resembles *L. persicus* and *L. stephensoni* in parapodial structure and setal type, but the pharyngeal areas V and VI differ from the above two species in having no processes. This specimen was collected from Australia, where

no *L. persicus* has been recorded. The available limited material does not allow a detailed analysis of the intraspecific variation in the pharyngeal areas of *L. stephensoni*. The specific status of this specimen is currently indeterminable.

In the *L. stephensoni* specimens examined, neuropodial falcigers are present from setiger 9–10 to the end of fragment (21–34 setigers), numbering 1–8 in upper fascicle and 3–15 in lower fascicle. In *L. persicus*, falcigers disappear on posterior neuropodia and it is not certain whether this is also true for *L. stephensoni*, because all specimens examined are anterior fragments and no previous reports of this species examined the occurrence of neuropodial falcigers along the body.

*Habitat.*—Rullier (1965) did not provide habitat information. According to Hutchings & Reid (1991), this species inhabits sandy mud.

*Distribution.*—Australia; Viet Nam.

*Leonnates nipponicus* Imajima, 1972

*Leonnates nipponicus* Imajima, 1972: 41–43, fig. 2A–L.

*Material examined.*—None. The type specimens (Holotype: NSMT-Pol. H74; Paratype: NSMT-Pol. P75) were not available for examination.

*Remarks.*—The original description is detailed and accompanied by figures of the head region, parapodia, and setae. This species is very similar to *L. indicus*. Imajima (1972) separated it from *L. jousseaumei* based on its distinctions in pharyngeal area III with 4 small soft papillae, instead of 6–7 chitinized paragnaths and notosetae as exclusively homogomph spinigers, instead of spinigers and a few homogomph falcigers posteriorly. Hutchings & Reid (1991) noted the more anteriorly disappearance of the notopodial supra-acicular ligule along the body of *L. nipponicus* than on specimens of *L. indicus*. As discussed previously, the pharyngeal area III of *L. indicus* contains 3–8 papillae that can be sclerotized to dif-

ferent extents (Table 1). Although the notopodial supra-acicular ligule of most of the *L. indicus* specimens we examined disappears only from far posterior segments, in two specimens this structure is absent before setiger 20 (Table 1). Notopodial falcigers, despite being few in each individual, have been found in posterior parapodia of all *L. indicus* specimens examined. The absence of notopodial falcigers in *L. nipponicus*, appears to differentiate it from *L. indicus*.

*Habitat*.—Corals.

*Distribution*.—Southern Japan.

*Leonnates crinitus* Hutchings & Reid,  
1991

Figs. 13, 14A–D

*Leonnates crinitus* Hutchings & Reid,  
1991: 50–52, fig. 2A–G.

*Material examined*.—Australia, Trinity Bay, Cairns, Queensland, (16°25'S, 145°27'E), intertidal, coll. Australian Littoral Society, 10 Dec 1974 (1 incomplete paratype) (USNM 123355); Wangewanja Cove, Port Essington, Northern Territory (11°23'S, 132°09'E), intertidal, 13 Sep 1985 (1 incomplete specimen) (NTM W3348).

*Description*.—The holotype (QM GH4683) was not available for examination. All three type specimens were from the same sample. Our description is based on paratype USNM 123355, a 26 mm long anterior fragment with 49 setigers.

Animal colour brownish with glandular region at base of dorsal cirrus. Prostomium pentagonal, not cleft on frontal margin. Antennae barely reaching joint between palphore and palpostyle. Two pairs of eyes in trapezoidal arrangement, anterior pair slightly larger. Peristomium with tentacular cirri, longest reaching back to setiger 8.

Pharynx half-everted with brownish, smooth jaws. Maxillary ring with paragnaths arranged as follows: area I = 4 in perpendicular row; II = 10 left, 11 right; III = 41; IV = 20 left, 19 right. Oral ring with

papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 8 in transverse row.

Parapodia of first 2 setigers with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule asetigerous, large, conical. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular lobe blunt. Neuropodial postsetal ligule with figure-like digit on upper tip. Ventral neuropodial ligule blunt, similar to neuropodial postsetal ligule. Ventral cirrus subulate, about as long as dorsal cirrus.

Remaining parapodia biramous with 6 ligules on anterior segments, 5 on posterior segments (Fig. 13A, B): dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule large, conical, slightly longer than notopodial supra- and infra-acicular ligules. Notopodial supra-acicular ligule blunt; of similar size to infra-acicular ligule (Fig. 13A); supra-acicular ligule gradually diminishing along body, but remaining distinct on last setiger of fragment; infra-acicular ligule taper in middle region. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular lobe blunt; postsetal ligule with figure-like digit on upper tip; finger-like digit reduced along body and absent from setiger 26. Ventral neuropodial ligule blunt anteriorly, elongated and pointing downward from setiger 23 (Fig. 13B). Ventral cirrus subulate, approximately as long as dorsal cirrus.

Notopodia with homogomph spinigers (Fig. 14A, B) throughout. Neuropodia with supra-acicular homogomph spinigers, infra-acicular heterogomph spinigers (Fig. 14C), heterogomph falcigers (Fig. 14D). Neuropodial spinigers present throughout, accompanied by falcigers in middle region. Neuropodial falcigers present from setiger 12–14 to setiger 42–48, numbering 1–2 in upper fascicle and 2–8 in lower fascicle.



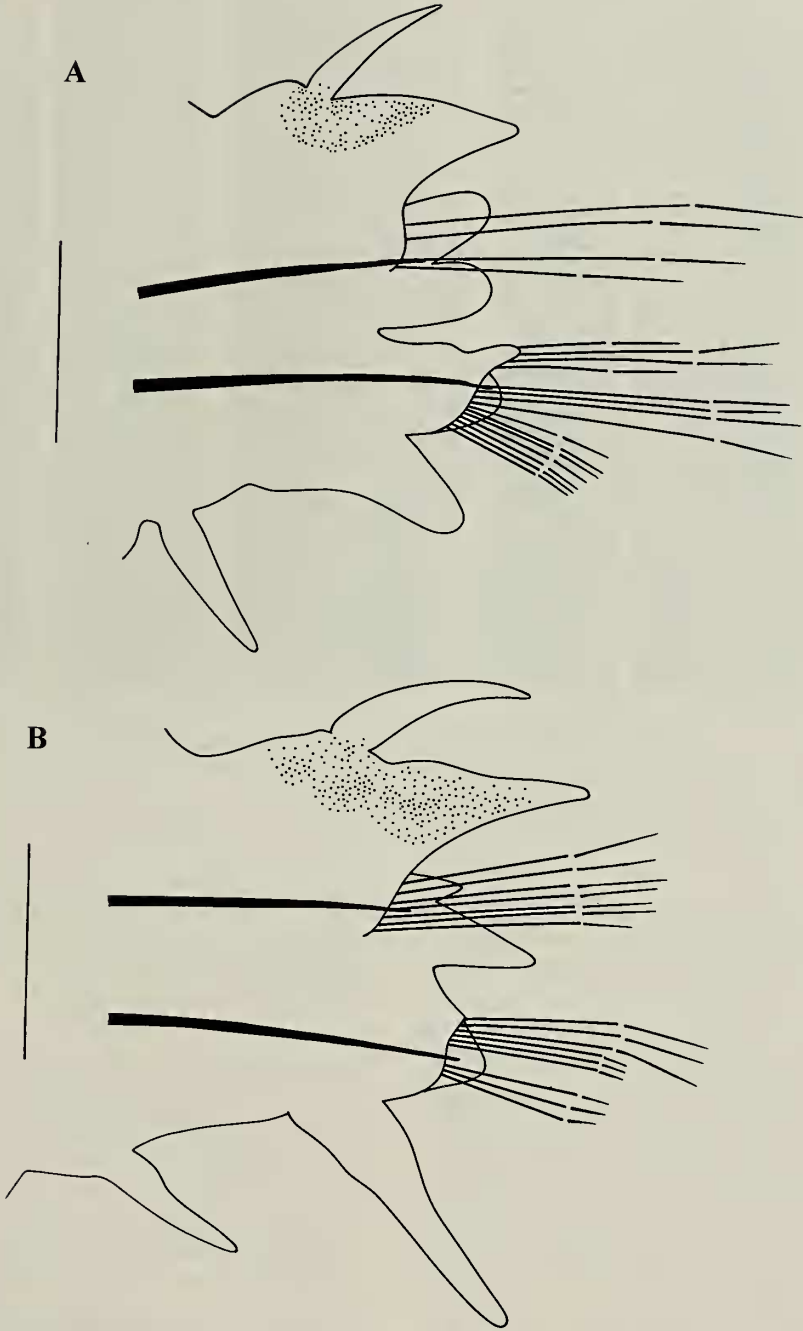


Fig. 13. *Leonnates crinitus* (Paratype USNM 123355). A. Posterior view of parapodium 8. B. Posterior view of parapodium 30. (Scale: A-B = 0.1 mm).

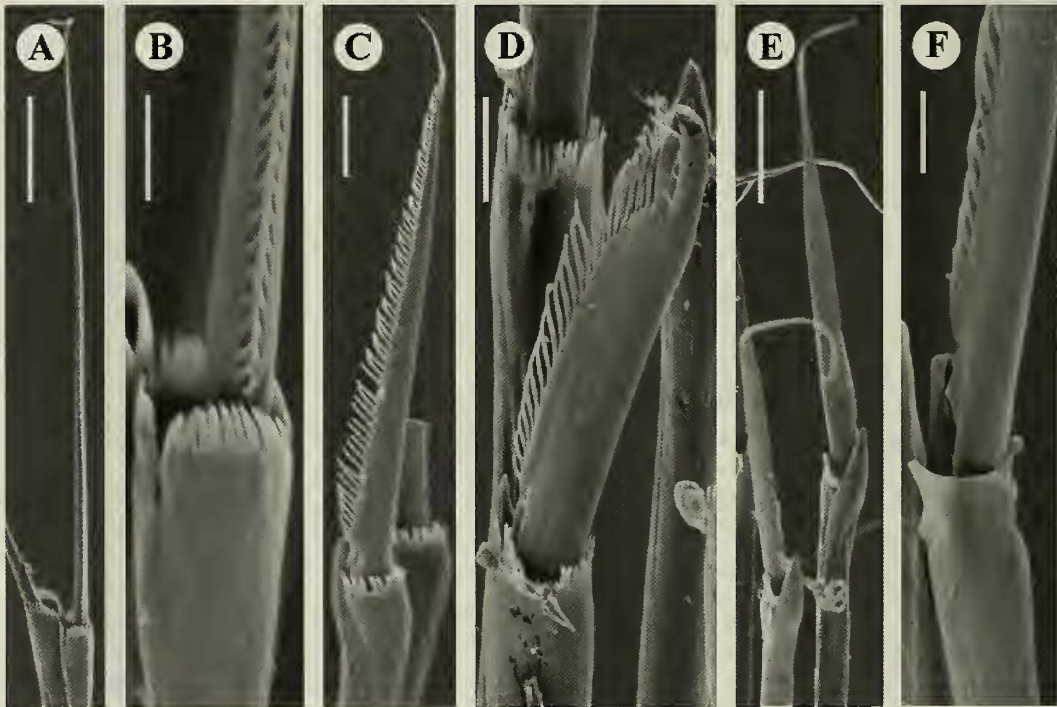


Fig. 14. *Leonnates crinitus* (Paratype USNM 123355). A. Notopodial homogomph spiniger from parapodium 30. B. Enlarged end of shaft of the spinigers in A. C. Neuropodial heterogomph spiniger from parapodium 8. D. Neuropodial falciger from parapodium 30. *Paraleonnates bolus* (USNM 127644). E. Notopodial spinigers from parapodium 4. F. Enlarged end of shaft of another notopodial spiniger from parapodium 4. (Scale: A = 20  $\mu$ m; B = 4  $\mu$ m; C = 20  $\mu$ m; D = 10  $\mu$ m; E = 20  $\mu$ m; F = 5  $\mu$ m).

*Remarks.*—The characters of the both specimens match well with the original description by Hutchings & Reid (1991). *Leonnates crinitus* is similar to *L. decipiens* in the shape of parapodia and in pharyngeal armature on areas II, IV, and VI, but differs from the latter in having 4–5 paragnaths, instead of none, arranged in a single perpendicular row on area I and a greater number of paragnaths (24–41 vs. 3–21) on area III. The spinigers and falcigers of these two species are also similar, except that heterogomph spinigers, observed in *L. crinitus* (Fig. 14C), were not found in *L. decipiens*. Homogomph falcigers in neuropodial supra-acicular fascicle of *L. crinitus*, reported by Hutchings & Reid (1991, fig. 2G) were not found. This difference, however, may be due to the limited material for SEM observation.

*Habitat.*—This species inhabits muddy

sand, 0–5 m; specimen NTM W3348 was collected from a rotting bark (Hutchings & Reid 1991).

*Distribution.*—Australia.

Key to the *Leonnates* species based on atokous specimens

- 1. Oral ring with paragnaths on area VI . . . . . *L. simplex*
  - Oral ring with only papillae . . . . . 2
- 2. Falcigers present on all neuropodia . . . . . 3
  - Falcigers not present on anterior neuropodia . . . . . 4
- 3. Posterior notopodia without falcigers . . . . . *L. nipponicus*
  - Posterior notopodia with few falcigers . . . . . *L. indicus*
- 4. Pharyngeal area V with papilla(e), papillae on area VI–VIII forming continuous rows . . . . . *L. stephensoni*
  - Pharyngeal area V without papillae, bor-

- der between areas VI and VII-VIII clearly defined ..... 5
5. In all parapodia, ventral neuropodial ligule slightly shorter than neuropodial acicular ligules ..... *L. persicus*
- In middle and posterior parapodia, ventral neuropodial ligule much longer than neuropodial acicular ligules ..... 6
6. Pharyngeal area I without paragnaths, area III with 3–21 paragnaths *L. decipiens*
- Pharyngeal area I with paragnaths, area III with 24–41 paragnaths ..... *L. crinitus*

*Australonereis* Hartman, 1954

*Australonereis ehlersi* (Augener, 1913)

*Nereis* (*Leonnates*) *ehlersi* Augener, 1913: 142–145, fig. 12A–C, pl. 3, fig. 53.

*Leptonereis ehlersi* Monro 1938: 618–623, fig. 7–13.

*Australonereis ehlersi* Hartman 1954: 19–23, fig. 1–11; Hutchings & Reid 1990: 77–78, fig. 4.

*Material examined*.—Swan River, Western Australia, (19 specimens) (ZIM V-7906).

*Description*.—None of the type specimens has an everted pharynx. The parapodia and setal structure match well with Hartman (1954). The pharyngeal structure, as revealed by examination of three specimens that have been dissected, also matches Hartman (1954). The tips of pharyngeal papillae are not sclerotized.

*Remarks*.—*Nereis* (*Leonnates*) *ehlersi* was originally described as having papillae on the oral ring and paragnaths on the maxillary ring (Augener 1913). Monro (1938) found papillae on the maxillary ring only, but he assigned this species to *Leptonereis*, which has a smooth pharynx. *Nereis* (*Leonnates*) *ehlersi* was later assigned to *Australonereis ehlersi* by Hartman (1954). *Australonereis* has a smooth oral ring and a papillate maxillary ring; its notosetae are spinigers and neurosetae are spinigers and falcigers. Hutchings & Reid (1990) provided a detailed description for specimens collected from different parts of Australia. They reported that the tips of the papillae

on the pharynx are sclerotized, and the sclerotization was not seen in all specimens they examined, but it was common and seemed to be independent of gender, size, and locality.

*Habitat*.—Muddy sand and sand flats.

*Distribution*.—Australia.

*Websterinereis* Pettibone, 1971

*Websterinereis glauca* Pettibone, 1971

*Leonnates pusillus* Langerhans, 1880: 279, pl. 14, fig. 10.

*Leptonereis glauca* Claparède, 1870: 454, pl. 7: fig. 3; Fauvel, 1914: 163, pl. 12, figs. 5–23; Ramsay, 1914: 244, pl. 1, figs. 1–10.

*Laeonereis glauca* Hartman, 1945: 22.

*Websterinereis glauca* Pettibone, 1971: 27–30, figs. 14–16.

*Websterinereis tridentata* Fauchald 1977: 90.

*Material examined*.—Madeiras, (3 specimens) (NHMV 2162).

*Description*.—Very tiny nereidids (<0.5 cm long), fragile after long storage. Pharynxes not everted. Dissection of one of the specimens revealing no chitinized paragnaths, but other details of pharyngeal structure were not observable. All tentacular cirri missing. Parapodia, except first two pairs, biramous, with no signs of heteronereidid modification. Throughout shape of parapodia and pattern of setal distribution similar. Notoetae homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers. Sex of specimens indeterminable.

*Remarks*.—*Leonnates pusillus* can not be assigned to *Leonnates* because it does not have both papillae and paragnaths on the pharynx. In the original description *L. pusillus* was depicted as having papillae on both rings, but it was afterwards referred to *Leptonereis glauca* Claparède, 1870 by Fauvel (1914) and Ramsay (1914); *Leptonereis* has a smooth pharynx. Later it was referred to *Laeonereis glauca* by Hartman (1954); *Laeonereis* has tufts of papillae on both pharyngeal rings. Afterwards it was



referred to *Websterinereis glauca* by Pettibone (1971); *Websterinereis* has a smooth maxillary ring and a papillate oral ring. Pettibone (1971) considered *L. pusillus* to be the male heteronereidid form of *W. glauca*, although Langerhans' sample also includes atokous specimens. Fauchald (1977) redefined *Websterinereis* as having a smooth maxillary ring and paragnaths on the oral ring, with *W. tridentata* considered as the sole valid species.

Our observations do not clarify to which genus these specimens belong, but there is no reason for us to state that they are not *W. glauca* as stated by Dr. Pettibone.

*Habitat*.—Types from old fish cages.

*Distribution*.—Madeiras.

*Paraleonnates* Chlebovitsch & Wu, 1962

*Paraleonnates bolus* Hutchings & Reid,  
1991

Fig. 14E–F

*Leonnates bolus* Hutchings & Reid, 1991:  
48–50, fig. 1A–E.

*Material examined*.—Holotype, 1 complete specimen from East Arm, Darwin Harbour, Northern Territory, Australia (12°30'S, 130°55'E), 2.5 by 50 mm, 115 setigers, 14 Dec 1984 (NTM W2518); paratype, 1 incomplete specimen from Port Warrender, Admiralty Gulf, Western Australia (14°35'S, 125°53'E), 2.8 × 45 mm, 86 setigers, Oct 1976 (USNM 127644).

*Description*.—Unless otherwise stated, our description is based on specimen NTM W2518. Pharynx with paragnaths on maxillary ring and papillae on oral ring, arranged as follows: area I–II = 35 paragnaths in 2 continuous irregular rows; III–IV = 48 paragnaths in 3 continuous irregular rows; V = 0; VI = 2 papillae, one blunt on centre of area, another sharply pointed located near frontal margin of oral ring; VII–VIII = 4 sharply pointed papillae, in transverse row, located near frontal margin of oral ring. Border between areas I and II and border between areas III and IV not clear. Paragnaths on middle of both dorsum and

ventrum of maxillary ring are slightly smaller than those on sides. Centre of area VII–VIII with some dermal folds (Fig. 1B in Hutchings & Reid 1991) but 4 blunt papillae, described on centre of oral ring (Hutchings & Reid 1991), not observed. Similar pharyngeal arrangement in specimen USNM 127644 as follows: areas I–II = 26 paragnaths in 2 irregular rows; III–IV = 34 paragnaths in 3 irregular rows; IV = 7 paragnaths; V = 0; VI = 1 sharply pointed papilla, located near frontal margin of oral ring; VII–VIII = 4 sharply pointed papilla in one transverse row, located near frontal margin of oral ring; on both areas I–II and III–IV, paragnaths on centre slightly larger than those on sides; border between areas I and II and border between areas III and IV not clear. No blunt papillae observed on area VII–VIII.

Parapodia of first 2 setigers subbiramous with 2 aciculae, without notosetae, with dorsal notopodial ligule, neuropodial presetal supra-acicular ligule, neuropodial presetal infra-acicular ligule, neuropodial postsetal lobe, and ventral neuropodial ligule. Dorsal notopodial ligule conical, asetigerous. Dorsal cirrus subulate, extending beyond dorsal notopodial ligule. Neuropodial presetal supra- and infra-acicular ligules conical. Neuropodial postsetal lobe broad. Ventral neuropodial ligule conical, slightly shorter than neuropodial acicular ligules. Ventral cirrus slender, shorter than dorsal cirrus.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial infra-acicular ligule, neuropodial supra-acicular ligule, neuropodial infra-acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule conical, as long as notopodial infra-acicular ligule. Dorsal cirrus slender, longer than dorsal notopodial ligule. Anterior neuropodia with presetal supra-acicular ligule, infra-acicular ligule, and postsetal ligule. Shapes of notopodial presetal acicular ligules similar along body, but postsetal ligule digit-form in anterior segments but absent

from setiger 39 in holotype and setiger 25 in specimen USNM 127644. Ventral neuropodial ligule smaller than neuropodial presetal acicular ligule. Ventral cirrus slender, shorter than dorsal cirrus.

Notopodia and neuropodia with heterogomph spinigers (Fig. 14E–F) throughout. Ends of shaft smooth, hinge with large tooth facing cutting edge of blade. Blade with fringe of small teeth on cutting edge. Smooth, long-bladed heterogomph falcigers in subacicular fascicle of far anterior parapodia, reported from the other paratype (WAM 422–86) in original description (Fig. 1H in Hutchings & Reid 1991), not found in holotype or paratype USNM 127644.

*Remarks.*—Our examination of the type and non-type specimens of *P. uschakovi* (about 20 specimens, IOCAS 08181, 09188) shows that the prostomium, the pharynx, the parapodia and the setae of *L. bolus* all resemble those of *P. uschakovi*. The original description of *P. uschakovi*, however, does not clearly show a digit-form neuropodial postsetal ligule. The papillae on the oral ring of *P. bolus* also agree well with those of *P. uschakovi*. *Paraleonnates uschakovi* has 1 sharp papilla and 1 blunt papilla on area VI, and 4 sharp papillae and 0–5 blunt papillae on area VII–VIII; the first row of paragnaths on area VII–VIII is sclerotized to higher degree than are those of second and third rows, while in *P. bolus* all paragnaths are quite well sclerotized. This difference may differentiate *P. bolus* from *P. uschakovi*. In the original description of *L. bolus*, one paratype (WAM 422–86, not available for examination) was shown to have long-bladed falcigers on anterior setigers, but neither the other types have such falcigers. Blunt papillae on the centre of oral ring are common to *Leonnates*, but the sharply pointed papillae near the frontal margin of the oral ring have not been reported in any other *Leonnates* species. The shaft of the spiniger of *P. bolus* differs from that of all *Leonnates* species in having a smooth end, instead of being fringed with teeth. The neuropodia of *P.*

*bolus* differ from those of all *Leonnates* species in having two presetal ligules and a postsetal lobe, instead of one acicular lobe or ligule and one postsetal lobe or ligule. Substantial differences between *Leonnates* and *Paraleonnates*, and the similarities between *P. uschakovi* and *L. bolus* suggest that *L. bolus* be transferred to the genus *Paraleonnates*. *Paraleonnates bolus* is distinguishable from *P. uschakovi* in higher degree of sclerotization in the second and third rows of paragnaths on pharyngeal area VII–VIII.

*Habitat.*—Mangroves (Hutchings & Reid 1991). Holotype from inside mounds made by burrowing lobster *Thalassina squamifera* de Man.

*Distribution.*—Northern Australia.

## Discussion

Generic separation in Nereididae has been mainly based on the pharyngeal structure and the types of setae present. Intra-generic variation of these characters has been noted (Fauchald 1977). Our examination of all available *Leonnates* species has allowed the assessment of such variation in *Leonnates*. In the pharynx of most *Leonnates* species, the maxillary ring has only sclerotized paragnaths and the oral ring has only soft papillae. However, there are exceptions: in some specimens of *L. indicus*, pharyngeal area III has soft papillae; in *L. simplex*, the pharyngeal area III has sclerotized paragnaths. The pharyngeal structure also serves to differentiate *Leonnates* from its closely related *Paraleonnates*; there are pointed papillae and blunt papillae on the oral ring of *Paraleonnates*, the former located near the upper margin, while the later located on the centre; in *Leonnates* there are only blunt papillae on the oral ring, located on the centre. Intraspecific variation in pharyngeal structure also exists: the extent of sclerotization of paragnaths vary in *L. indicus* specimens of collected from the same population. Previous descriptions of pharyngeal area VII–VIII of

*Leonnates* reported rows, rather than exact numbers of papillae present. Our study reveals that, at least in *L. indicus* and *L. persicus*, the number of papillae present on this area is positively related to the body size, suggesting that the number of rows of papillae alone may not be an effective character for species separation in *Leonnates*.

Six types of setae have been reported in Nereididae (Pettibone 1963, Chambers & Garwood 1992): compound homogomph spiniger; compound heterogomph spiniger; compound homogomph falciger; compound heterogomph falciger; compound paddle-shaped seta; and simple falciger. Of these, simple falciger, which is found on the posterior neuropodia of *Neanthes diversicolor* (Müller, 1776), is a specialized compound falciger whose blade is fused to the shaft. The other five types of setae have been observed in *Leonnates*. Except the paddle-shaped seta, which occurs only in heteronereidids, the other four types of setae found in *Leonnates* share a common character, i.e., the end of shaft has a large tooth, which is fringed by a circle of smaller teeth. This character also serves to differentiate *Leonnates* from *Paraleonnates*, which has a smooth end of setal shaft. However, there are substantial intrageneric difference in the setal blades of *Leonnates*; in *L. indicus*, the blade is convex with short teeth; in other species the blade is fringed with slender teeth, and the shape varies from triangular in *L. simplex* to slender in *L. persicus*, *L. decipiens*, *L. stephensoni*, and *L. crinitus*.

Apart from pharyngeal structure and types of setae present, parapodial structure is also important in the generic identification of Nereididae (Pettibone 1971). In *Leonnates*, the neuropodia consist of an acicular lobe or ligule and a postsetal lobe or ligule; whereas in *Paraleonnates*, the neuropodia consist of two acicular ligules and a postsetal lobe or ligule.

At maturity, many nereidid species undergo significant changes in internal structures such as musculature and gut, and external structures such as parapodial lobes,

setae, prostomial sense organs, and in males, the pygidium. These changes lead to a special stage termed epitoke or heteronereidid with shorter body length, larger parapodia, and broad-bladed setae that aid swimming. The extent of epitokous modification differs from one species to another and between male and female of one species. According to their extent of epitokous modification and the associated mating behavior, nereidids can be divided into three groups (Pettibone 1963): one without an epitokous stage and swarming; ones with a slight epitokous modification but without distinct heteronereidids and with limited swarming activity; and ones with significant modified heteronereidids and active swarming activity. In *Leonnates*, both mature and immature individuals have been reported only in few species. *Leonnates niestrasi* and *L. insolitus* are known only from heteronereidids, while *L. simplex*, *L. nipponicus*, *L. crinitus*, *L. stephensoni* are known only from immature individuals. Heteronereidids of *L. niestrasi* (male), *L. decipiens* (male), *L. insolitus* (female), *L. persicus* (male) have significant modified eyes, parapodial ligules and setae. The females of *L. indicus* and *L. persicus*, both with mature oocytes, however, have no significantly modified external body structures. Based on the above limited information, no pattern of epitokous modification in *Leonnates* can be generalized.

In summary, our study shows that *L. virgatus*, *L. pusillus*, *L. jousseaumei*, *L. decipiens* var. *manilensis*, and *L. bolus* are not valid *Leonnates* species. *Leonnates virgatus* and *L. jousseaumei* are conspecific with *L. indicus*. *L. decipiens* var. *manilensis* is conspecific with *L. decipiens*. *Leonnates bolus* belongs to *Paraleonnates*. *Leonnates niestrasi* and *L. insolitus*, described from heteronereidids with highly modified parapodia and setae, can not be fully characterized. *Leonnates pusillus* is indeterminable to genus. Some specimens originally identified as *L. jousseaumei* are heteronereidids of *Perinereis*.



# Acknowledgments

We thank R. Sun for donating 4 non-types of *L. jousseaumei*; L. Ward, H. ten Hove, M. Nechama Ben-Eliahu and M. Kuper for assistance with some early literature; L. Gosselin, E. Bourget, T. Harder, M. Beckman, M. Hopkins and H. Otto for translating some literature; A. Wiktor, A. Brandt, D. Eibye-Jacobsen, M. Petersen, P. Hutchings, G. Dally, M. Lowe, J. Bleeker, M. Hewitt, K. Sindemark, J. van der Land, Y. P. Lam, C. M. Yang, L. Ward, K. Fauchald, P. Barents, S. Halsey, H. Sattmann, F. Pleijel, and M. J. d'Hondt for arranging specimen loans; L. Cui, S. Cheung, S. Shek, and S. Leung for assistance with graphics; P. Garwood, G. Paterson, M. Kendall, and J. J. Kan for helpful discussions; C. Eldridge for proof-reading. The thoughtful comments and criticisms by P. Garwood, G. Paterson, T. Perkins, and an anonymous reviewer have led to a substantial improvement of the manuscript. Specimens of *Leonnates persicus* from Hong Kong were collected by ERM Hong Kong Ltd. under a contract from the Civil Engineering Department of Hong Kong. This research was supported by grant ERM 95/96.SC01 to P.Y.Q.

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